Flexibility in antipredator behaviour of Tasmanian macropods to altered devil abundance

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DECLARATION

This thesis, to the best of my knowledge, contains no material which has been previously published or written, except where due reference has been given in text, and contains no material which has been accepted for the award at any university or tertiary institution.

STATEMENT OF ETHICAL CONDUCT

This research was conducted following guidelines approved by the University of Tasmania Animal Ethics Committee (Animal Ethics Approval Number: A0017756). The authority to disturb wildlife for scientific purposes was approved by the Department of Primary Industries, Parks, Water and Environment, Tasmania (Authority No: FA 18278)

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TABLE OF CONTENTS

1. **Abstract**

Trophic cascades have been occurring at an increased rate due to the global decline of top predators. Top predators are important in maintaining the biodiversity of ecosystems through their top-down influence on prey species, both consumptive via predation which affects population vital rates and behavioural in response to the risk of predation. Predator presence and density is known to have strong influence on prey behaviour and demographics. Antipredator, or risk-sensitive, behaviours of prey individuals reflect their perceived level of threat in the environment. Behavioural responses in prey to changes in predator abundance, either declines or increases, can happen after a relatively short periods exposure (weeks or months). However, the expression of such behaviours will vary between species and individuals, depending on factors such as ecological niche, body-size and age. The flexibility of prey behaviour can therefore indicate the perceived level of risk, predator-induced or otherwise, in the environment.

A rare opportunity to study the simultaneous effects of top predator decline and increase is afforded by the natural decline of the Tasmanian devil (*Sarcophilus harrisii*) from a novel infectious disease across its distributional range in Tasmania, Australia, and an assisted translocation for conservation of the devil to an offshore island. Tasmanian devils have drastically declined in abundance in the past two decades due to the transmissible devil facial tumour disease, with some areas of the state reduced to only 5% of the original devil population. Devil decline has already begun to have an impact on the behaviour of prey species in the environment but is likely to cause greater effects to the ecosystem balance as the disease continues to spread across Tasmania. To provide a wild-living insurance population, in the event of extinction of the devil in the wild, a disease-free population of devils was introduced onto Maria Island, a historically devil-free island and National Park 5km off the east coast of Tasmania.

To determine the influence of devil abundance on Tasmanian macropod antipredator behaviours, three types of antipredator behaviour were studied (vigilance behaviour, flight initiation distance and emergence time and distance from cover) following the loss and gain in abundance of devils. The three species studied, the Tasmanian pademelon (*Thylogale billardierii*), Bennett's wallaby (*Macropus rufogriseus*) and Forester kangaroo (*Macropus giganteus tasmaniensis)*, are all susceptible to predation from Tasmanian devils, but due to species differences will express different levels of risk-sensitive behaviours. Macropod behaviours were compared at three sites with distinct devil abundances using both historic and novel data sets collected 'before' and 'after' changes in Tasmanian devil abundance.

Top predator pressure proved to have little influence on the expression of antipredator behaviours in macropods. No universal changes were seen among all species in response to devil decline or increase over time. However, changes in the structural complexity of the environment (vegetation regrowth) had a strong influence on risk-sensitive behaviour, irrespective of devil abundance. Species ecology, body size (between species and within species) and age also influenced the expression of antipredator behaviours of macropods. Smaller prey animals (both due to species body size and age) are most vulnerable to predation. This vulnerability was reflected in their anti-predator behaviour which did not reflect changes in predator pressure. Larger species are more influenced by vegetation changes than predator abundance changes. These results illustrate the complex and multifaceted relationship between predator and prey and the need for more comprehensive studies on interspecies relationships to prevent further loss of top predators in the natural environment

2. **Introduction**

Top predators play a fundamental role in shaping prey behaviour and sustaining ecosystem health (Duffy et al., 2007, Ritchie and Johnson, 2009). Top or apex predators are those positioned at the top of the food chain without any predators themselves. Thus, they can have strong top-down effects, both direct consumptive or predatory, or non-lethal and indirect pressures, on other species in the ecosystem (Elmhagen and Rushton, 2007, Estes et al., 2011). Such pressures have powerful influence on the abundance and behaviour of prey species (Brown et al., 1999, Barbosa and Castellanos, 2005). Predation directly affects population dynamics and selection pressures through mortality. Non-lethal pressures influence behaviour, shaping a species temporal and spatial use of the environment to avoid the risk of encountering a predator (Lima, 1998). Non-lethal pressures are mediated via changes in abundance or behaviour of other species. This can include altered competitive relationships and effects of predators, or the competitive release of mesopredators, resulting in increased predation. Top predator effects cascade across multiple trophic levels, with the potential to alter food-webs and control vegetation structure and interspecies dynamics (Portalier et al., 2019, Wallach et al., 2015, Strong and Frank, 2010). To understand the influence of top predators on an ecosystem and its species, it is essential to study the behaviours of their prey.

Predation risk-sensitive behaviour in animals

Animal behaviour is labile which allows animals to rapidly respond to novel environmental stressors (Foster, 2013, Gross et al., 2010, Adams et al., 2006). Antipredator behaviours are short-term behavioural responses which are phenotypically plastic and can develop rapidly in response to innate threats (Bize et al., 2012, Blumstein et al., 2002). Prey species develop a variety of antipredator behaviours depending on the type and intensity of the predation threat (Chivers et al., 2016). Antipredator behaviours, such as sheltering in vegetation or highly vigilant activity, will influence foraging rates, habitat use and reproductive success of prey (Manning et al., 2009, Ripple and Beschta, 2004, Barros et al., 2016).

Vigilance behaviour is a way in which animals detect cues by collecting and inferring information about the surrounding environment to determine the intensity of risk (Parsons et al., 2018, Lima and Dill, 1990). It is defined as standing or crouching with head up in a position that allows scanning of the environment for potential threats such as predators (Elgar, 1989). Improving the ability to detect cues in the environment increases the chance of a prey individual successfully responding to cues and evading or escaping predation (Lima and Bednekoff, 1999). Emergence time and distances from cover at different times of the diel cycle reflect the temporal niche of major predators in the

environment. In smaller species, closer proximity to cover ensures a quick escape to safety to avoid detection from predators. For larger species which often forage in groups, greater emergence distances from cover enables prey to detect predators emerging from cover sooner, allowing more time to flee (Banks, 2001). The frequency and amount of time for spent vigilant represents an individual's perceived level of risk of threats such as predation in its environment. Fearful or anxious animals will allocate more energy and time to acquiring information about their surroundings than to other behaviours, such as foraging (Olson et al., 2015). As vigilance and foraging are mutually exclusive behaviours, being vigilant results in trade-offs, where one behaviour forgoes time allocated to the other (Blumstein and Daniel, 2005, Brown and Kotler, 2004). This reduction in foraging activity can have healthy impacts on individuals, including declines in growth or reproductive success (Brown et al., 1999).

The time allocation and microhabitat use for foraging is further explained by the 'landscape of fear' (LOF) concept, in which prey habitat selection is determined by the perception of predation risk (Laundré et al., 2010). Predators create a LOF in which prey will be finely tuned to assess the level of risk of encountering a predator and modify their behaviour accordingly (Bleicher, 2017). As predation intensity and predator diversity is ever-changing in the ecosystem, so does the LOF (Kohl et al., 2018, Bleicher, 2017). Prey behaviour is expected to reflect changes in perceived environmental risk while balancing other physiological needs and alternate opportunities. This explains why dehydrated animals are more likely to risk predation by drinking at predator frequented watering holes (Bleicher, 2017, Blumstein and Daniel, 2003). Flight initiation distance of a prey individual, in relation to an approaching predator, reflects the general level of threat perceived by the animal from predators in its environment (Price, 2008). Starved animals have shorter FIDs Conversely, prey species in higher LOF will risk missed mating or feeding opportunities for safety (Brown et al., 1994, Brown, 1988, Adams et al., 2006).

An animal's perceived level of threat in its environment is also related to its ecological niche, body size and age. Smaller species which are more susceptible to a greater host of predators will have a greater perceived level of risk than larger, less vulnerable species (Werner and Gilliam, 1984). Younger animals are not only generally smaller than adults, but are also less experienced and naïve to predators, therefore at more risk of predation (Abrams and Rowe, 1996). Prey animals must be able to learn mechanisms, from personal experience or from conspecifics, in order to overcome the threat of predation.

Loss and recovery of top predators globally

The increasing loss of top predators in natural ecosystems is contributing to the accelerated rate of decline in global biodiversity (Duffy, 2003, Ripple et al., 2014). Changes in top predator abundance can trigger trophic cascades, in which their influence affects more than one level in the ecosystem (Wallach et al., 2015, Schmitz et al., 2010, Beschta and Ripple, 2009, Estes et al., 2011). Trophic cascades can involve the competitive release of mesopredators (those predators that have predators themselves), leading to the increased predation on and decline of populations of small prey species, or increases in large herbivorous species, both of which result in an overall reduction in biodiversity (Prugh et al., 2009, Ripple et al., 2016). An overabundance in larger herbivores causes over-browsing or over-grazing of vegetation, reducing vegetative cover which is important for smaller mammals, birds, and invertebrates for food or protection from predators (Ritchie and Johnson, 2009, Ripple and Beschta, 2008).

The global decline of top predators consequently increases the frequency of trophic cascades in marine and terrestrial environments (Estes et al., 2011, Morris and Letnic, 2017). For example, a reduction in the population of elasmobranch-consuming sharks (*Carcharhinus spp.*) in the Atlantic has caused the proliferation of cownose rays (*Rhinoptera bonasus*), resulting in the loss of bay scallops (*Argopecten irradians*) from the ecosystem (Myers et al., 2007). In Australia, many marsupial species including burrowing bettongs (*Bettongia lesueur*) and greater bilbies (*Macrotis lagotis*) are threatened by extinction by invasive mesopredators in habitats lacking dingoes, the top predator (*Canis lupus dingo*) (Johnson et al., 2007). Dingo-free areas lack mechanisms for controlling the populations of invasive mesopredators, such as feral cats (*Felis catus*) and foxes (*Vulpus vulpus*), which decimate native species populations, making it more difficult to maintain a balanced healthy ecosystems (Newsome et al., 2015, Dickman, 1996, Woinarski et al., 2015).

The re-establishment or reintroduction of top predators is effective in facilitating recovery of biodiversity in an ecosystem, however, it is less common (Elmhagen and Rushton, 2007, Ripple et al., 2014). In recent times, the passive recovery of top predators such as of leopards (*Panthera pardus*) in Asia, and brown bears (*Ursus arctos*) and lynx (*Lynx lynx*) in Europe, has begun to occur (Chapron et al., 2014, Athreya et al., 2013). Lynx recovery throughout Europe has occurred in response to government regulation of hunting lynx, with recovering populations associated with highly productive environments (Linnell et al., 2009). The reintroduction of wolves (*Canis lupus*) into historic ranges has occurred in North America to reduce over-browsing by herbivores and restore the natural landscape. Wolves controlled elk (*Cervus elaphus*) densities, allowing for the selective release of vegetation which had been previously overgrazed and overbrowsed. This increased the

abundance of ecologically important animals such as beavers (*Castor canadensis*) and bison (*Bison bison*)(Ripple and Beschta, 2012, Ripple and Beschta, 2003, Ripple and Beschta, 2004). The introduction of predators to naïve ecosystems within potential, but outside historic range, is rare as it can cause detrimental effects on the ecosystem. However, the recent translocation of a top predator, the Tasmanian devil (*Sarcophilus harrisii*) onto Maria Island, an island off the east-coast of Tasmania, has been successful (DPIPWE, 2011, Ingram, 2019).

Loss and introduction of top predators in Tasmania

Tasmania, a large continental island (68,400 km^2) to the south of the Australian mainland, has the greatest assemblage of marsupial carnivores globally (Jones, 1995). The extinction of the largest marsupial top predator, the thylacine (*Thylacinus cynocephalus*), in the 1930s, resulted in some restructuring of the food web, with the Tasmanian devil (hereafter, devil) becoming the largest and top predator within the Tasmanian ecosystem (Carlson et al., 2018). Devils although relatively small in size (7-14kg), are the largest extant marsupial predator (Lachish et al., 2009, Menkhorst and Knight, 2004, Jones, 2008). They are morphologically specialised scavengers. but are also effective predators, consuming a wide range of prey species dominated by macropods, particularly Tasmanian pademelons (*Thylogale billardierii*), as well as brushtail possums (*Trichosurus vulpecula*) and common wombats (*Vombatus ursinus*) (Jones, 2003, Jones and Barmuta, 1998, Andersen et al., 2017, Pemberton et al., 2008). Although they have a wide source of prey and no natural predators, devils have undergone severe population decline in the last 20 years due to a novel transmissible cancer (Lazenby et al., 2018).

Devil facial tumour disease (DFTD) was first detected in north-east Tasmania at wukalina/Mt William National Park in 1996, and has spread across much of the devil's range in Tasmania, reducing populations by an average of 80%, with local declines of up to 95% (Storfer et al., 2018, Pease and Wayne, 2014). Narawntapu National Park, in the centre of the north coast of Tasmania, only had the first of detection of DFTD in 2007, over a decade after DFTD was first discovered (Epstein et al., 2016, Hawkins et al., 2006). Progressive population declines of devils have resulted in a reduction in top-down effects in the Tasmanian ecosystem and an increase in mesopredators, specifically feral cats and black rats (*Rattus rattus)* (Hollings et al., 2015a). This has had cascading influences on other native, species in the ecosystem, including the loss of native small mammals (Hollings et al., 2015a). In areas of intact forest habitat, high abundance of healthy devil populations may be able to indirectly maintain healthy populations of native mesopredators by suppressing populations of feral species, such as feral cats (Hollings et al., 2014). In agricultural areas, devils have less influence in suppressing cats as these are highly productive systems appear to be driven more strongly by rainfall

and abundance of invasive prey such as rabbits (*Oryctolagus cuniculus*) (Hollings et al., 2014, Elmhagen and Rushton, 2007, Brashares et al., 2010). High feral cat abundance has shown to have a negative relationship with both species of quolls (*Dasyurus spp.*), with cats breeding faster and potentially outcompeting spotted-tailed quolls (*D. maculatus*) and preying on eastern quolls (*D. viverrinus*), particularly juveniles (Cunningham et al., 2018, Fancourt et al., 2015). As a specialised scavenger, devils efficiently remove carrion from the landscape, reducing the spread of disease and limiting access to other mesopredators via resource competition, including invasive and native mesopredators such as forest ravens (*Corvus tasmanicus*) and spotted-tailed quolls (Cunningham et al., 2018, Hollings, 2013, DPIPWE, 2011).

Devil decline not only influences species demographics, but also has direct correlations with the loss of devil-specific antipredator behaviours in prey. Brushtail possums observed in areas with over 90% devil population decline had similar giving up densities (GUDs) to possums surveyed in predator-free environments, and spent more time foraging on the ground, further away from vegetation cover and trees (Hollings et al., 2015b). GUD is the density of resources available in a foraging patch when an animal decides to stop feeding and leave the area. A decline in GUDs indicates there is a reduction in the LOF of the environment (Brown, 1988). The erosion of experience-dependant behaviour, such as GUDs is not uncommon in environments lacking predation pressures and can occur relatively rapidly following predator decline (Blumstein, 2006, Blumstein and Daniel, 2005).

Tasmania provides two natural experiments on the effects of top predators in ecosystems. In parallel to the progressive decline in devil populations from DFTD, devils were introduced as an 'assisted colonisation' (as per IUCN/SSC (2013)) to Maria Island in 2012 (Rogers et al., 2016). The National Park, 5km off the east coast of Tasmania, acts as a conservation action to create a free-living insurance population of healthy DFTD-free devils (Wells et al., 2019, Lazenby et al., 2018, Thalmann et al., 2015, DPIPWE, 2011). The introduction of devils makes it possible to simultaneously study the effects of decline and introduction of the same top predator to its natural ecosystem.

While devils were probably present on Maria Island prior to sea level rise at the beginning of the Holocene (~11,500 years before present), they are not recorded there in the last 200 years (Lambeck and Chappell, 2001, Rounsevell et al., 1991, Brüniche-Olsen et al., 2014). Prey species of devils were exposed to the predation threat from devils for the first time in 2012 (Ingram, 2018, Rogers et al., 2016, Jones and McCallum, 2007). With over 50 faunal species inhabiting Maria Island, including threatened and migratory species, the introduction of this top predator established a new LOF (Cunningham et al., 2019a, Jones and McCallum, 2007). Devils are expected to increase the biodiversity of the ecosystem by controlling feral cat abundance and preventing the overpopulation

of major prey species, possums and macropods, (DPIPWE, 2011). The behaviour of prey species on Maria Island reflected low perceived levels of risk due to the absence of top predator pressures. Macropods had suffered from overpopulation and overgrazing in the past, resulting in the need for annual macropod culling to sustain viable, healthy populations (Ingram, 2018). The establishment of devils has resulted in some flexible changes in behaviour in their prey. Temporal shifts in prey behaviour have occurred in wombats and Bennett's wallabies (*Macropus rufogriseus)*, with increased early morning/late afternoon foraging and reduced foraging at night, during peak devil activity (Cunningham et al., 2019b, Cunningham et al., 2019a). Brushtail possums have also shown an increase in risk-sensitive behaviour on Maria Island since devil introduction, having higher GUDs in areas of high devil density (away from human interference) (Cunningham et al., 2019a). As all seven species of macropod inhabiting Maria Island have been found in devil scat throughout Tasmania, I expect to potentially see greater behavioural flexibility and antipredator behaviour expression in these species (Jones and Barmuta, 1998).

Macropod species on Maria Island range in body size from 1kg long-nosed potoroos (*Potorous tridactylus*) to 60kg Forester kangaroos (*Macropus giganteus tasmaniensis*) (Jones and McCallum, 2007). The Tasmanian pademelon and Bennett's wallaby are the species most susceptible to devil predation prey due to their intermediate body size and foraging behaviour in fragmented landscapes, the preferred habitat of devils (Jones and McCallum, 2007, Ingram, 2018, Clauss et al., 2008, Andersen et al., 2017). Potoroos are preyed on by devils but are possibly too small to be major prey. Forester kangaroos are much larger and spend more time in open grasslands, but are still potential prey to devil, whether that be by scavenging carcasses of adults, or hunting smaller, younger individuals (Andersen et al., 2017, Pemberton, 1990, While and McArthur, 2006, Wiggins and Bowman, 2011). By studying three macropod species, Tasmanian pademelon, Bennett's wallaby and Forester kangaroo, all of which forage in open grasslands, but encompass a range of body sizes, I can determine the influence of body size and species ecology on the antipredator behaviour of free-ranging macropods.

Bennett's wallabies and Tasmanian pademelons are widespread throughout Tasmania, and Forester kangaroos are present throughout the eastern half of the state (Menkhorst and Knight, 2004). All three species of macropod rely on a range of cues for predator detection, including olfactory, visual and chemosensory cues (Blumstein et al., 2002, Mella et al., 2014, Lima and Dill, 1990). Tasmanian pademelons are predominantly browsers, foraging in more densely vegetated areas than larger species. It is characteristic for pademelons to hide in vegetation during daylight hours and emerge into the open to forage from dusk till dawn (While & McArthur, 2006). Bennett's wallabies, an intermediate-sized species, are both browsers and grazers. They spend the majority of their time in

the safety of vegetation cover, but emerge from cover earlier in the afternoon and return to dense vegetation later in the morning than pademelons, overlapping with Forester kangaroo emergence behaviours (Clauss et al., 2008, le Mar and McArthur, 2005). Forester kangaroos are grazers and can be observed out in the open for most of the day as their morphology (larger, longer legs), equips them better to flee rather than hide from predators. Nocturnal emergence patterns of these three species reduces the contact of these macropod species with devils during their peak temporal niche (Pemberton, 1990, le Mar and McArthur, 2005, While and McArthur, 2006).. By studying changes in emergence times and distances from cover over time, I can determine if any correlations in this behaviour relate to devil abundances.

Timescales of change are challenging to study in wildlife as it is difficult to consistently monitor a wild population of animals without observers indirectly influencing their behaviours. Species can undergo behavioural changes within a matter of months or over several generations depending on the species and the flexibility of the behavioural response (Carthey and Blumstein, 2018, Jolly et al., 2018). Short to medium-term changes (taking weeks to months to change) can be accomplished by behavioural plasticity or cross-generational learning (Foster, 2013, Renn and Schumer, 2013). Loss of behaviours can occur relatively quickly when the predation pressure is reduced or lost (Blumstein, 2006). Both these mechanisms can rapidly generate change to maintain the survival of prey populations when novel environmental pressures arise (Bytheway and Banks, 2019, Westrick et al., 2019). As a result, the environmental pressures of a specific time period will influence the expression of antipredator behaviour of prey during that time. This basis of understanding makes it possible to compare behaviours of prey animals in environments of contrasting time periods and threats, which in the case of this study, focuses on changes in devil abundance.

Objective and aims

The overarching objective of this project is to determine if macropods are responsive, in their risk-sensitive behaviour, to changes in the density of a major predator, the Tasmanian devil. I capitalise on a study system, whereby field research was conducted in three National Parks prior to major changes in devil density. The three National Parks contrasted in the patterns of change in devil abundance, with devils declining from DFTD at one site (Narawntapu), devils introduced to another (Maria Island), and no change in devil abundance at the third (wukalina/Mt William). I refer to previous data sets collected in 2001 and 2009 as the 'before' period. I repeated the research in 2019, matching methods, species and sites, and refer to this as the 'after' period. I analyse the data together in a before-after control-impact study design of pre- and post-devil abundance changes (Blumstein and Daniel, 2003, Menkhorst and Knight, 2004). The outcomes of this research will be

used to answer specific questions about the influence of environmental and individual parameters on the anti-predator strategies of prey species.

Risk-sensitive behaviours will vary with the environmental context and species ecology. The influence of species, body size and age of individuals of the three macropod species, and the environmental context in which the behaviours were observed, such as distance from cover or time of day, also influence risk and risk-perception. These were measured and incorporated in statistical models as predictors of the response variables to better understand the influences of risk-sensitive behaviours. Three types of risk-sensitive behaviour were studied: vigilance behaviour, flight initiation distance and, emergence time and distance from cover. Vigilance was measured through direct observations of macropods, to determine the perceived level of risk of the individual in its environment. Flight initiation distances were measured by approaching macropod individuals to quantitatively compare the wariness of individuals between sites. Emergence time and distances from cover were obtained through walking-line transects to demonstrate the LOF of the environment, and the influence of diel cycles on response behaviours.

This temporal framework of different histories of devil density over a 10-18 year period, at three sites, three species and three behaviours may provide the opportunity to predict the flexibility of macropod behavioural changes in response to modified predation threats. It will contribute to understanding the ecological role of devils in the Tasmanian ecosystem and help improve the scientific understanding of Tasmanian predator-prey interactions.

3. **Methods**

3.1 Study site and study species

The study was carried out at three sites across Tasmania, spanning an 18-year period which included changes in devil population density at two of the three sites during the second decade. The study sites were wukalina/Mount William National Park in the far northeast of Tasmania, Narawntapu National Park on the central north coast and Maria Island National Park off the east coast of Tasmania (sites hereafter referred to as wukalina, Narawntapu and Maria) (Figure 3.1). All three sites have a mosaic of dry eucalypt forest and woodland interspersed with areas of open grassland that were modified from the original vegetation for agriculture, either livestock pasture or cropping. All three sites are at sea level (Narawntapu 8m, Maria 14m, wukalina 20m) with similar mean temperatures (min 10^{o}C max 17^{o}C) and rainfall (520-750mm/year) (Bureau of Meteorology, 2019).

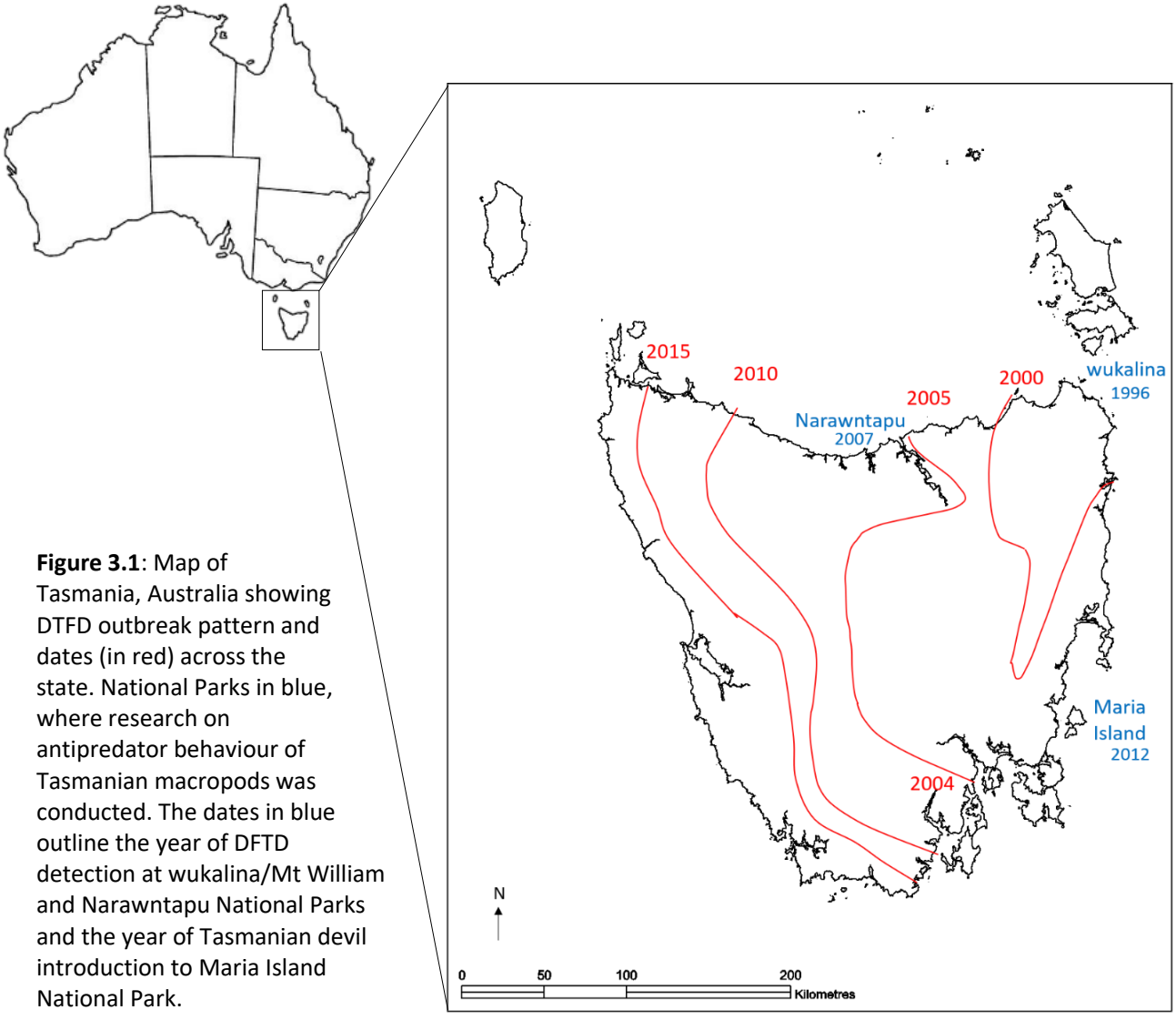

Figure 3.1: Map of Tasmania, Australia showing DTFD outbreak pattern and dates (in red) across the state. National Parks in blue, where research on antipredator behaviour of Tasmanian macropods was conducted. The dates in blue outline the year of DFTD detection at wukalina/Mt William and Narawntapu National Parks and the year of Tasmanian devil introduction to Maria Island National Park.

Two prior studies on predation risk-sensitive behaviours of three species of macropods were carried out in the 2000s: field work conducted in 2001 by Blumstein and Daniel (2003) and in early 2009 by Nielsen (2009). The species studied in these projects were the Forester kangaroo (*Macropus giganteus tasmaniensis)*, Bennett's wallaby (*Macropus rufogriseus*) and Tasmanian pademelon (*Thylogale billardierii*) (hereafter, kangaroo, wallaby, pademelon). These species range in size with pademelons being the smallest (females: 5kg, males: 8kg), wallabies (females: 15kg, males: 25kg) and the largest, kangaroos (females: 35kg, males 65kg) (Menkhorst and Knight, 2004). All species of macropod were present at the three sites, although there was slight variation in the abundance of each species among sites. At all sites, devils are the predominant terrestrial mammalian predator of macropods however, aerial avian predators, the wedgetail eagle (*Aquila audax*) and white bellied sea eagle (*Haliaeetus leucogaster*) are also present and prey on macropods (Simpson et al., 2004).

The study was designed to assess the response, in risk-sensitive behaviours, of each of the three macropod species to changes in devil density that occurred in the 10-year period up to 2019. The two studies by Blumstein and Daniel (2003) and Nielsen (2009) provided the 'before' component and my study, in 2019, the 'after' component in a BACI or 'before-after-control-impact' design. Each study site had a different history of change in devil abundance over the last decade. The devil population has remained stable at low density at wukalina for the last 20 years (Lazenby et al. (2018)), following the first detection of DFTD in Tasmania at wukalina in 1996 (McCallum et al., 2009, Hawkins et al., 2006) (Figure 3.1). Thus, wukalina served as the 'control' site where devil density did not change during the study period, including from 2001 ((Blumstein and Daniel, 2003) to 2009 (Nielsen, 2009) and to 2019 when my field work was conducted. At Narawntapu, the earlier studies by Blumstein and Daniel (2003) and Nielsen (2009) were conducted when devil populations were at the pre-disease high population level (Lazenby et al., 2018). The first case of DFTD was documented in October 2007 (Epstein et al. (2016) but prevalence was initially low and devil population density remained high until 2010, with substantive population decline after 2009 (Lazenby et al., 2018). Devil abundance only begins to rapidly decline three years after local DFTD emergence, reaching an average decline of 77% after 5 years of DFTD being present in the population (Lazenby et al., 2018). In 2019, 12 years after disease emergence, devil densities were low.

On the offshore island of Maria Island National Park, a number of species of wildlife, including kangaroos and wallabies (pademelons were present at the time of European settlement), brushtail possums and devils have been introduced (PWS, 1998, Rounsevell, 1985). Devils were first introduced in 2012 (Rogers et al., 2016) (Figure 3.1). Prior to 2012, the macropods on the island had not been exposed to the threat of predation by devils. Blumstein and Daniel (2003) and Nielsen (2009) conducted research on Maria prior to devil introduction, surveying macropods in a predator-

free environment (excluding aerial predators). Since 2015, devils on Maria Island have reached their carrying capacity population of around 100 devils on the 9,672 ha island (Ingram, 2018, Rogers et al., 2016). My study at Maria in 2019 thus represents high devil density.

Field trips were conducted during the Austral summer, following the procedures of Blumstein and Daniel (2003) and Nielsen (2009), to ensure that environmental variables that might influence macropod behaviour, such as day length and temperature, were similar during all data collection periods. Between January and April 2019, two 10-day field trips were carried out at both wukalina/Mt William National Park and Maria Island National Park and three week-long field trips were conducted at Narawntapu National Park. This difference was due to logistics and time management constraints such as National Park schedules and volunteer availabilities. Of these fieldtrips, one fieldtrip at each site was conducted in January 2019 as a pilot study; not all data collected from these fieldtrips was included for analysis.

3.2 Field methods

Three different risk-sensitive behaviours were observed to account for the various ways in which macropod behaviour may have changed in response to changes in devil abundance. Each method focused on one aspect of antipredator behaviour: vigilance behaviour, flight initiation distance and emergence time and distance. These methods were based on the techniques used by Blumstein and Daniel (2003) and Nielsen (2009). This allowed direct analytical comparisons to be made between the 'before' and 'after' periods of data collection. Wet and windy weather are known to increase vigilant or anxious behaviour in some mammals, so no data was collected in substantive rain or when the wind was more than 40 km/h, (McDonough and Loughry, 1995, Hayes and Huntly, 2005).

Observations of vigilance behaviour

Behavioural observations of macropods were conducted by making five-minute video recordings of focal animals foraging in the open. Observations were made in three time periods representing key periods for foraging that have different risk of predation. These were during the morning (5 – 9 am), afternoon (6 – 9 pm) or night (9 pm – 2 am). The aim was to survey equal numbers of adult and subadult, and male and female animals for each species. Only individuals foraging in open habitat was selected for observation. After a settling period of at least five minutes, a video recording of the focal animal was taken using a SONY Handycam (model: HDR-CX625). At night, a FLIR thermal imaging monocular (model: Scout II 640) was used to scan the surroundings to find macropods and identify a focal individual. Videos were then recorded using a light intensifier (Pyser-SGI PNP Night

Vision Pocket Scope) with Pentax 80 mm lens attached to the video camera. All recordings were made at least 1 km away from human activity, including camp grounds. Observations were made in different parts of the three National Parks on different days to avoid oversampling the same groups of macropods and to minimise the chance of resampling the same individuals. These methods followed Blumstein and Daniel (2003), who provided more detailed methods than Nielsen (2009).

At the time of the video recording in the field, the following metadata were collected: the date, time of day (morning, afternoon or night), species, sex (if able to determine, otherwise recorded as unknown), age, conspecific group size at 10 and 50 metres and the distance the animal was from vegetation cover (the forest edge). Age was determined by the size of the individual in comparison to other conspecifics in the vicinity. If it there was any uncertainty in its age, it was assumed to be an adult. Videos were analysed back in the laboratory using the program *JWatcher* (Blumstein et al., 2006, Blumstein and Daniel, 2007), to quantify time spent in different activities. A range of behaviours were recorded from the videos, including vigilant, feeding, locomoting and grooming behaviours.

Testing Flight Initiation Distance (FID)

Previous studies have shown that FID, the distance at which an animal flees from an oncoming predator, indicates the flightiness of a prey individual (Price, 2008, Blumstein et al., 2003). Humans have been used in the past as an effective replacement of a predator to test FID in prey species (Price, 2008, Blumstein et al., 2003). More fearful individuals will have a greater FIDs in order to allocate themselves enough time to flee from predators (Duffy, 2003, Ydenberg and Dill, 1986). Individuals were approached with calculated paces at 0.5 metres/second to determine their flight initiation distance (FID), as per the methods used by Blumstein and Daniel (2003) (Nielsen (2009) did not collect FID data). The number of paces was later used to calculate the distance between the observer and subject at three positions:

a. the distance when the subject oriented towards the observer,
b. the distance when the subject hopped away, and
c. the total distance between observer and subject at the starting position.

Only animals foraging in open grassland were approached. The date, time, species, sex, age, distance from cover, and group size (as for vigilance recordings) of each subject was noted. Site and species differences in FID are expected to reflect differences in predator exposure. To reduce the influence of human activities on macropod behaviour, animals were not sampled in areas of high human

activity, including in proximity to walking tracks and roads, campgrounds or other man-made disturbances.

Transect sampling

Walked line transects were used to collect data on the time of day that macropods emerged from the forest edge and the distance that they emerged into open grassland vegetation. Methods replicated those from Nielsen (2009) (Blumstein and Daniel (2003) did not collect emergence behaviour data and did not set up transects). Transects were set up the day before data was collected to reduce the influence of the disturbance of transect setting up on the behaviour of the macropods. All transects were set up between 1 - 10 km distance from human activity, roads or camping areas to reduce the risk of human interference with the transect sites. Transect 3 at Narawntapu national park was adjacent to a horse-riding trail, however, this was rarely used during the study period and not at all during data collection times.

Three transects were set up at wukalina and Narawntapu, and one, longer discontinuous transect was set up on Maria where the configuration of open areas was more constraining. Transects were situated on the forest edge of open grassland. A forest was defined as an area or woodland of dense vegetation where subjects could shelter or hide in and was sufficiently dense that observers could not see through to the other side of the vegetation. Transects were set up on flat ground so that the whole transect was visible from the walking line, to ensure that all macropods present in the survey area could be accounted for. To reduce the risk of re-sampling animals between transects, transects were at least 500 metres apart from one another and 150 metres away from the next forest. Due to vegetation regrowth over the past decade, it was not possible to replicate the exact transect locations as the original study in 2009 however, transects were set up as close to the original locations as possible. Vegetation regrowth also impacted the transect lengths at each site, leading to a slight variation in transect lengths between sites (Appendix A). At Narawntapu, dense vegetation in the middle of the transect sites fragmented the landscape. As this could have acted as shelter for smaller macropods, transects were split into two (a and b) to avoid these regrowth areas (Appendix B).

To set up the transects, wooden pickets were set up in a grid formation. Six to eight pickets were hammered into the ground near the forest edge at 45 metre intervals parallel to the forest edge. At each of these pickets, eight or nine additional pickets extended into the open grassland perpendicular to the forest at 15 metre increments. Reflective markers were attached to the pickets so they could be located at night. The picket locations were pre-calculated online using Google maps, then GPS coordinates were used to set them up in the field. Additionally, a tape measure was

used to ensure that pickets were the correct distance apart from one another, as it proved difficult to find exact GPS coordinates in the field. Transects were walked along the fifth line of pickets from the forest edge, approximately 75 m from the forest edge, although this distance varied from 60 – 90 m as the forest edges were not straight (Appendix B).

When walking the transects, the observer walked at a pace of 0.5 metres/second. This limited disturbance to animals on the transect and allowed enough time to thoroughly scan and spot subjects on the transect grid. When a subject was seen, the observer would stop and identify the species, age (adult or subadult), distance it was from cover and conspecific group size. The subject's location on the transect in relation to the parallel and perpendicular pickets was noted to determine the distance it had emerged from the edge of the vegetation cover.

Transects were walked during four biologically distinct time periods, in terms of foraging and predation risk, following methods from Blumstein and Daniel (2003). These times were: three hours before dusk (BD), dusk (D), night (N) and midnight (M). As these timeframes vary depending on the sun's cycle, there were no set hours for when transects were conducted. Instead, visual cues were relied on. Dusk was defined as the period when the sun began to set, just before it got too dark to see subjects clearly with the naked eye. In January, this was at 9 pm whereas in April it was around 7 pm. The BD transects occurred 3 hours before this, at 6 pm or 4 pm respectively. The N timeframe started as soon as the sky was pitch black and torches were needed to safely walk around in the dark (Jan = 10 pm, April = 9 pm). M transects occurred 2-3 hours after the N timeframe (between 12 – 1 am). During the BD timeslots, all transects were walked as there were generally few macropods present on transects at this time, so enough time was available to scan all three transects. For all other timeframes, only one of the three transects was walked. This reduced the risk of resampling individuals on transects throughout the night. It was important to keep track of the subjects which continued to travel through the transect during data collection to ensure they were not resampled further along on the transect. The main researcher walked and scanned transects at all sites to maintain consistency. This person was either Daniel Blumstein or Emilie Roure. A second person would assist and record the data.

During the N and M timeframes, a FLIR thermal imaging monocular (model: Scout II 640) and Zeus Assassin handheld LED red-light spotlight were used to identify the subjects on the transect. The FLIR monocular was more effective in identifying subjects which were further away. In windy weather, however, the thermal camera was not as reliable, so the spotlight was always on hand to use as well.

During the first three fieldtrips, only one pilot transect was set up at each national park. These transects were set up in a similar location as Transect 1 at each site (Appendix A). Each pilot transect

was walked once during each timeframe. In the following fieldtrips, each transect had at least two repeats per timeframe to increase the sample size of transects. Six nights were allocated to transect data collection for each site during the secondary fieldwork trips.

3.3 Data handling and statistical analysis

Data handling of historic data

The previous datasets by Blumstein and Daniel (2003) and Nielsen (2009) analysed their data through the use of different statistical programs. To make it easier to handle the data, for all datasets, historical and current, only raw data was used to analyse together using the statistical program R (R Core Team, 2019).

Matching datasets and data handling for analysis

To statistically compare the results of the two older data sets, the 'before' studies, with my 2019 'after' study required comparing like with like. In the study by Blumstein and Daniel (2003), not all species were observed at all sites (Table 3.2). Wallabies and kangaroos were observed at Maria and wukalina only, and pademelons only at Narawntapu. Nielsen (2009) and the 2019 dataset surveyed all species at all study sites.

	Blumstein & Daniel (2001)	**Nielsen (2009)**	**Roure (2019)**
wukalina/ Mt William National Park	 Bennett's wallaby Forester kangaroo	Tasmanian pademelon Bennett's wallaby Forester Kangaroo	Tasmanian pademelon Bennett's wallaby Forester Kangaroo
Maria Island National Park	 Bennett's wallaby Forester kangaroo	Tasmanian pademelon Bennett's wallaby Forester Kangaroo	Tasmanian pademelon Bennett's wallaby Forester Kangaroo
Narawntapu National Park	Tasmanian pademelon	Tasmanian pademelon Bennett's wallaby Forester Kangaroo	Tasmanian pademelon Bennett's wallaby Forester Kangaroo

Table 3.2: Macropod study species surveyed at National Park study sites for each dataset (and the year their data was collected).

Nielsen (2009) did not follow exactly the same methods to collect vigilance scores in the field, using a stopwatch to time behaviours, with an assistant recording behaviours and times directly on a paper data sheet. This would have led to less accurate times and time lags in recording. These differences became evident during exploratory data analyses and consequently her vigilance data were not included in further analyses (Appendix C). In 2019, pademelons were observed at all sites, however they were difficult to approach at wukalina to test FID as they were too flighty. This resulted in pademelon FIDs being tested at only two sites in 2019: Narawntapu and Maria.

Scoring of behavioural observations

More than 570 videos of macropod behaviour were recorded between January and April 2019. Videos selected for analysis were between 3-5 minutes duration and the focal individual was in view most of the time; those where the focal animal moved completely out of view before 3 minutes time were excluded from analysis. The amount of elapsed time allocated to each behaviour was quantified using JWatcher (Blumstein et al., 2006, Blumstein and Daniel, 2007). The focus behaviour for this study was vigilance which involved both 'rearing and looking' and 'standing and looking' behaviours. Other behaviours were categorised into foraging, locomotion, social or grooming behaviours. Foraging included standing (on all four legs) and rearing while foraging. Locomotion occurred in the form of pentipedal walking, hopping or running. If the animal moved briefly out of view but subsequently returned to view, the time spent out of view was subtracted from the total observed time. The same observer scored all of the recordings with JWatcher to reduce the chance of observer bias in data handling.

Analysis of vigilance behaviour

Proportional response variables present analytical difficulties because they are count data but unlike Poisson count data, both the number of events that did and did not occur are known (Crawley, 2015). We therefore modelled this proportional response variable within a generalised linear model framework by converting the data to a binomial family structure (Crawley, 2015). Fifty samples (n=50) from the data set for each video were used to determine the number of successes or failures (with regard to vigilant activity), where the number of successes = x and the number of failures = (n-x). Generalised linear mixed models (GLMMs) were then used to compare the influence of specific variables on the response variable: the vigilance behaviour of individuals. Predictor variables or fixed factors were age, site, observer, distance from cover, and time of day variables. The random factor was the replication represented by individual videos. A set of models were constructed that represented biologically plausible questions about how these predictor variables and combinations and interactions amongst them influenced vigilance.

Two sets of analyses were done. The first involved a comparison of the 2001 and 2019 datasets, to determine if there were differences in macropod behaviour over time (due to increase, decrease or sustained devil abundance). The second analysis focused solely on the 2019 dataset to make species-site comparisons and determine the influence of site on behaviour. Each macropod species was analysed separately. Multi-model inference was used to rank the models with Akaike's Information Criterion (AIC). AIC model weights, parameter effect size and relative importance of variables (sum of AIC weights for all models that included the particular variable) was used to determine the influence of the predictor variables on the proportion of time spent vigilant while foraging (Burnham et al., 2011b, Burnham and Anderson, 2002).

Analysis of flight initiation distance (FID)

Only individuals at least 10 metres away from the observer at the starting point were included in analyses. This was the minimum distance which Blumstein and Daniel (2003) used for their FID measurements. These data were analysed in two sets of GLMMs, with each macropod species analysed separately in both analyses. Model parameters included combinations and interactions between the site, observer, age, distance from cover, and time of day variables. The first method of analysis involved comparing the 2019 data with analogous 2001 (Blumstein & Daniel) species-site combinations. This set of analyses was important in determining if changes in predation pressure over a relatively short timescale are reflected in local prey antipredator behaviours. The second set analysed the data collected in 2019 independently, to quantify any species differences across sites. Hypothetically, this would illustrate the influence of environmental conditions on macropod antipredator behaviours.

Analysis of emergence time and distance from cover

Analyses of the data collected from the walking line-transects would produce results illustrating any changes in emergence from forest distance for foraging due to changes in devil abundance. These analyses were conducted using GLMMs (similar to those used for analysis of the vigilance behaviour). Both sets of data (2019 and 2009) were analysed concurrently to determine the emergence distances and times for each species/site combination. Each macropod species was analysed separately. Emergence distance was analysed using GLMMs to determine which predictor variables influenced macropod behaviour. Model parameters included combinations and interactions between the site, observer, age and timeslot (time of day) variables. Emergence time was determined through comparing species/site/timeslot combinations and analysing the frequency of each species emerging from cover during each timeslot.

4. **Results**

4.1 Vigilance

Comparative analyses of 2001 and 2019 data sets

Pademelons: Time of day was the most influential factor on vigilance behaviour at Narawntapu although the influence of time of day varied with observer (time period). As observer and time period ('before-after' comparison) are directly confounded, future references to 'observer' in the results will relate to time period differences. Time of day was the top model, carried an AIC weight of 0.521 and had a relative importance amongst the variables of 0.993 (Table 4.01). The interaction term between time of day and observer also had high influence on vigilance, with a ΔAIC of 1.24 but an AIC weight of only 0.280. All other models had little influence on vigilance (ΔAIC < 6)(Richards, 2008). Pademelons were most vigilant in daylight during the morning and decreased activity in the afternoon, with the lowest proportion of time spent vigilant at night (Figure 4.01). This diel pattern of vigilance varied with observer, with the proportion of time spent vigilant decreasing in the afternoon as devil density declined and increasing slightly (overlapping confidence intervals) at night between 2001 when devil density was high and 2019 when it was low. There were few morning observations of pademelons in 2019 (reflected in the large confidence intervals) and none in 2001.

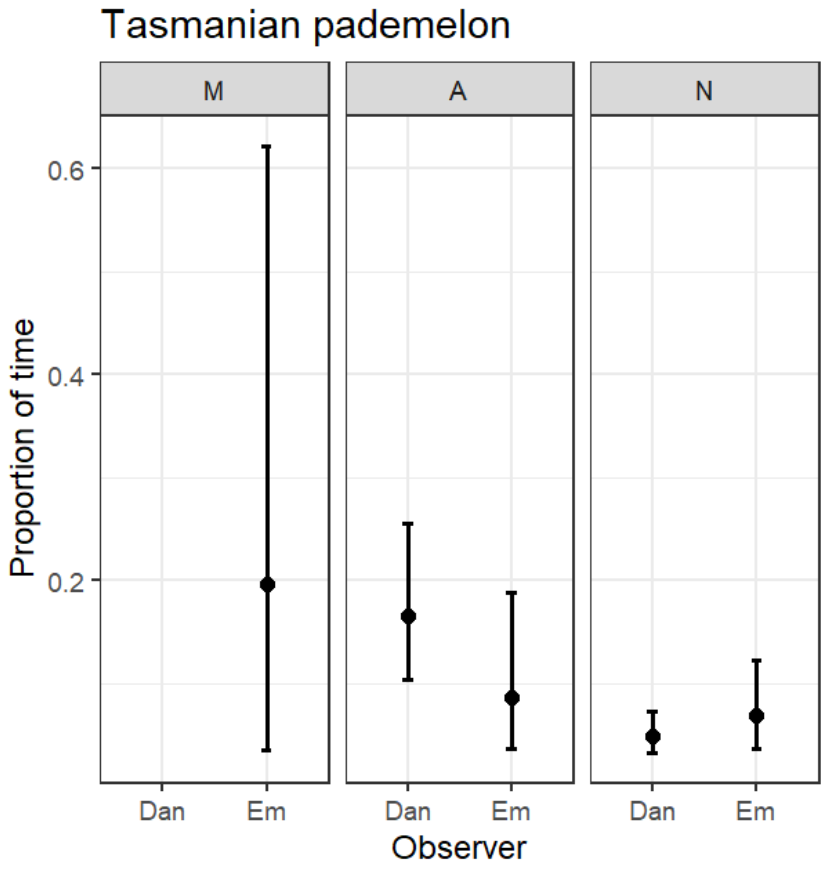

Figure 4.01: Plot of the interactive effects of time of day and observer on the proportion of time spent vigilant in Tasmanian pademelons observed at Narawntapu National Park in 2009 (Dan Blumstein) and 2019 (Emilie Roure). Columns: M = morning, A = afternoon, N= night.

Wallabies: Vigilance varied amongst sites and the pattern across sites was different between observers, suggesting that site and observer were the most influential factors. The top model, which holds all of the AIC weight, was the interaction term between site and observer (Table 4.01). All other models carried little weight (ΔAIC > 6)(Richards, 2008). Vigilance scores were higher at Maria for both observers than at wukalina. Additionally, at wukalina, wallabies observed in 2019 showed a greater proportion of time spent vigilant than those observed in 2001 (Figure 4.02). The relative importance variables (RIV) showed that both site and observer are the most important variables, both with an RIV of 1.

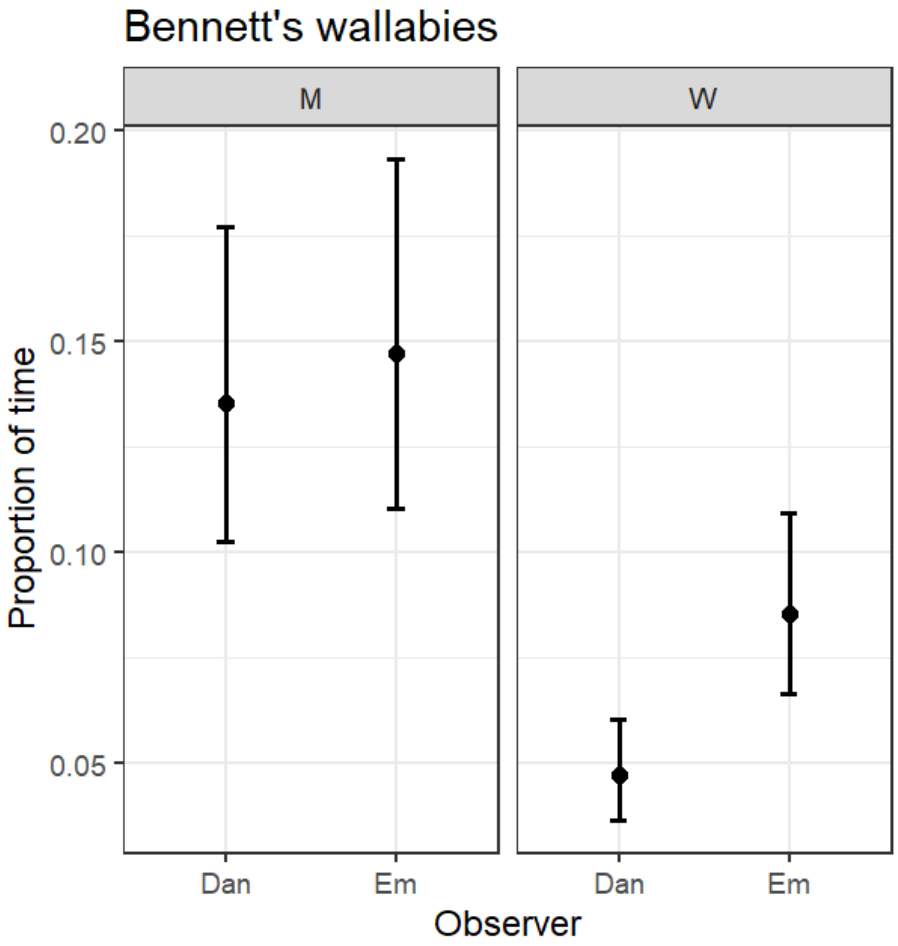

Figure 4.02: Plot of the site and observer effect on the proportion of time spent vigilant in Bennett's wallabies observed at Maria Island (M) and wukalina/Mt William (W) National Parks in 2009 (Daniel Blumstein) and 2019 (Emilie Roure).

Kangaroo: Vigilance behaviour was most influenced by site factors with kangaroos being more vigilant at wukalina than at Maria. Observer also had some influence, as kangaroos showed a slight reduction in vigilance at both Maria and wukalina in 2019 (Figure 4.03). All the models tested were influential of the response variable with ΔAIC units < 6 from the top model (Table 4.01). The top model, the univariate model with the site parameter, held 47% of the total model AIC weight. The second model, less than 2 ΔAIC units from the top model was a multivariate model involving site and observer and carried 18% of the total model AIC weight. Observer had some influence on the response variable as this has a RIV value of 0.381, although site had the greatest influence with an RIV of 0.852.

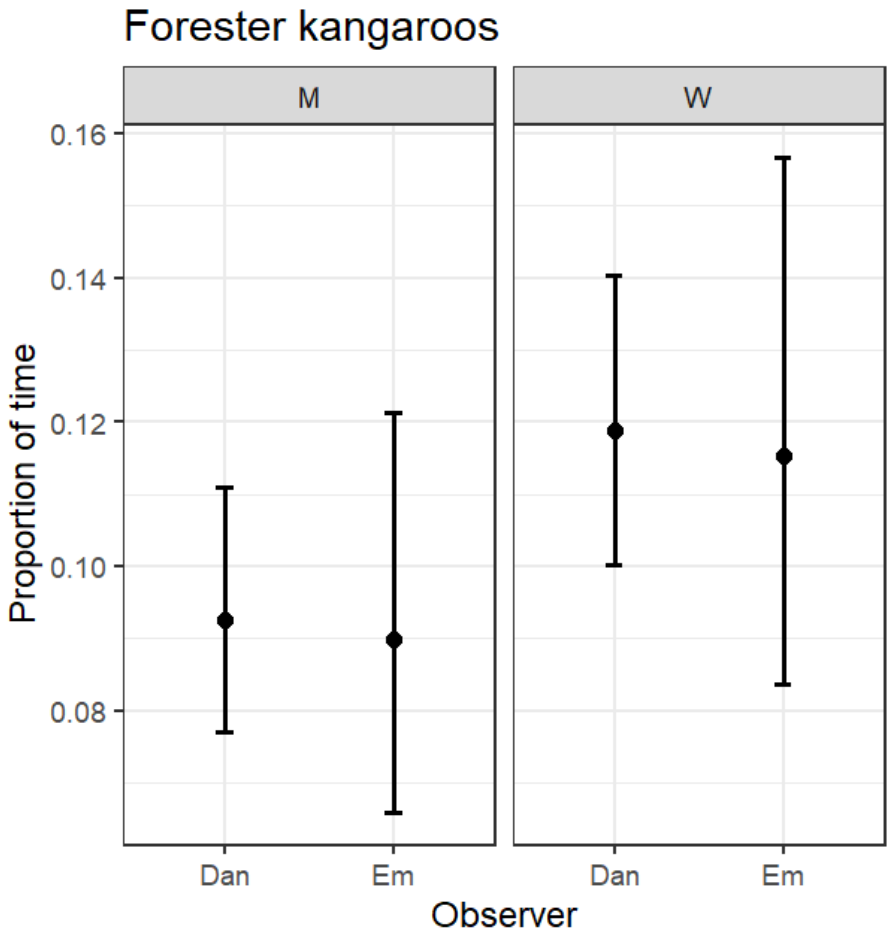

Figure 4.03: Plot of the site and observer effect on the proportion of time spent vigilant in Forester kangaroos observed at Maria Island (M) and wukalina/Mt William (W) National Parks in 2009 (Daniel Blumstein) and 2019 (Emilie Roure).

Table 4.01: Final model set from GLMM of vigilance behaviour of Tasmanian pademelons (Narawntapu National Park), Bennett's wallabies and Forester kangaroos (Maria Island and wukalina/Mt William National Parks) observed in 2001 and 2019 in Tasmania, Australia.
Model parameters: O= observer, S= site, T= time of day, A= age, D= distance from cover.
Parameter estimates ± Standard Error (SE) are included for each parameter in every model.

Model	Inter-cept	O	S	T	A	D	O*S	O*D	O*T	AIC	∆ AIC	AIC Weight
PADEMELON												
T	-1.407	—	—	-0.413 ± 1.010	—	—	—	—	—	979.8	0.00	0.646
T*O	-1.759	0.353 ± 0.387	—	0.145 ± 1.083	—	—	—	—	-1.094 ± 0.658	981.1	1.24	0.348
null	-2.494	—	—	—	—	—	—	—	—	989.0	9.22	0.006
RIV		0.378	0.000	0.994	0.000	0.000	0.000	0.000	0.348			
WALLABY												
S*O	-1.853	0.096 ± 0.232	-1.153 ± 0.209	—	—	—	0.541 ± 0.300	—	—	2152.4	0.00	1
T+O	-2.212	0.288 ± 0.172	—	-0.430 ± 0.186	—	—	—	—	—	2183.8	31.38	0.000
T*O	-2.082	0.108 ± 0.301	—	-2.08 ± 0.256	—	—	—	—	0.229 ± 0.379	2187.1	34.69	0.000
null	-2.371	—	—	—	—	—	—	—	—	2191.4	38.97	0.000
RIV		1.000	1.000	0.000	0.000	0.000	1.000	0.000	0.000			
KANGAROO												
S	-2.289	—	0.281 ± 0.134	—	—	—	—	—	—	3616.0	0.00	0.471
S+O	-2.282	-0.034 ± 0.179	0.279 ± 0.134	—	—	—	—	—	—	3618.0	1.96	0.177
null	-2.149	—	—	—	—	—	—	—	—	3618.4	2.33	0.147
S*O	-2.260	-0.142 ± 0.235	0.236 ± 0.147	—	—	—	0.255 ± 0.362	—	—	3619.7	3.47	0.083
S+D+O	-2.267	-0.040 ± 0.185	0.274 ± 0.141	—	—	-0.018 ± 0.154	—	—	—	3619.9	3.95	0.065
S*O + A	-2.330	-0.115 ± 0.253	0.238 ± 0.147	—	0.072 ± 0.252	—	0.247 ± 0.363	—	—	3620.0	5.39	0.032
S + D*O	-2.259	-0.065 ± 0.261	0.274 ± 0.141	—	—	-0.028 ± 0.170	—	0.050 ± 0.364	—	3620.1	5.93	0.024
RIV		0.381	0.852	0.000	0.032	0.089	0.115	0.024	0.000			

Analysis of 2019 dataset

Pademelons: Pademelons expressed a high level of vigilance irrespective of any of the parameters measured. However, age and site had some influence as subadult pademelons were slightly more vigilant than adults, and pademelons were most vigilant at Narawntapu (Figure 4.04 and 4.05). The null model, being the top-ranked model, had a 40% total AIC weight (Table 4.02). All of the models tested were within ΔAIC < 6 of the top model indicating that all parameters tested had some influence on the proportion of time spent vigilant (Richards, 2008). The top three models carried 76% of the AIC model weight and were within 2 ΔAIC values of the top model, indicating high influence on the response variable (Burnham et al., 2011a). The second model, the univariate model of the age parameter, was only 0.87 ΔAIC units different from the top model had an AIC model weight of 24%. The third model, also a univariate model of the site predictor variable, had an AIC total model weight of 15%. Other models included time of day with an AIC model weight <10% (ΔAIC of 2.79), and all further models had model weights <10%. The relative importance of variables indicated that age (RIV = 0.33) and site (RIV = 0.29) were the most important variables.

Wallabies: Vigilance activity of was influenced the most by time of day. Wallabies observed during early hours of the morning spent a greater proportion of their time vigilant than those observed at night. Site also influenced vigilance levels with the lowest rate of vigilance behaviour observed at wukalina. Age also had some influence, with subadult wallabies having greater vigilance scores than adult wallabies (Figure 4.06). The top ranked model was the multivariate model with site and time of day and carried 69% of the total AIC model weight (Table 4.02). The second model, a multivariate involving three parameters, site, age and time of day, carried 30% of the total AIC model weight and was within 2 ΔAIC units from the top model. All other models were > 6 ΔAIC units from the top model and weighed less than 10% of the total model weight, so had little influence on the response variable. The relative importance of variables confirmed that the most influential variables were time of day (RIV = 0.992) and site (RIV = 0.988).

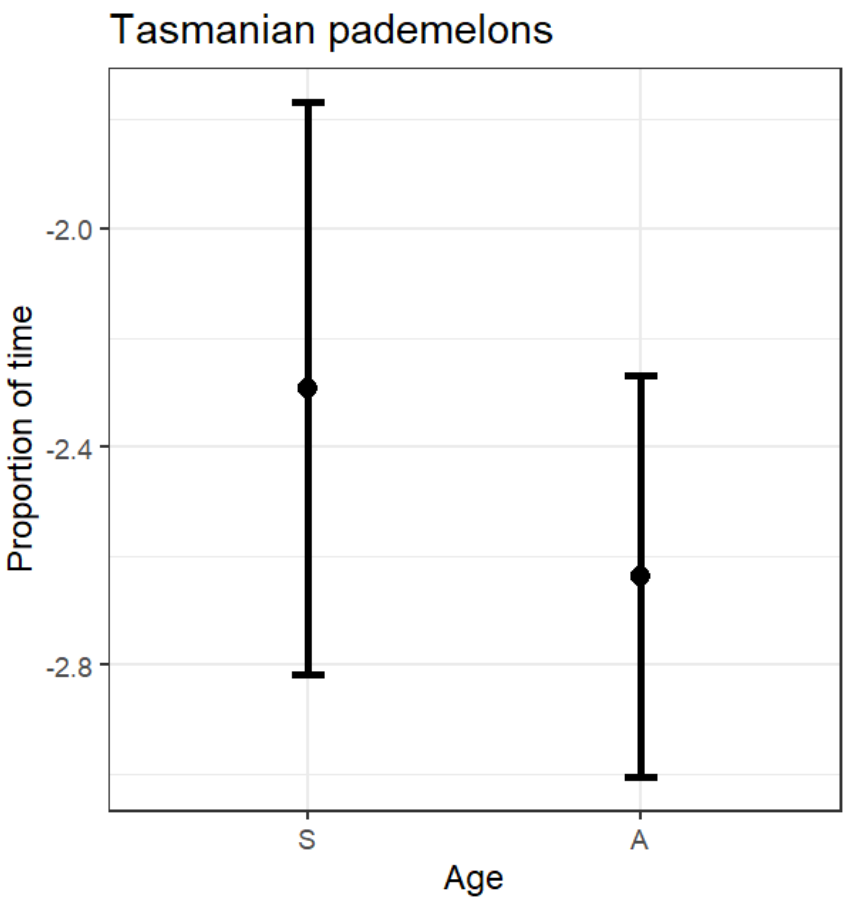

Figure 4.04:
Plot of the age effect on the proportion of time spent vigilant in Tasmanian pademelons observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.
Age: S= subadult, A= adult

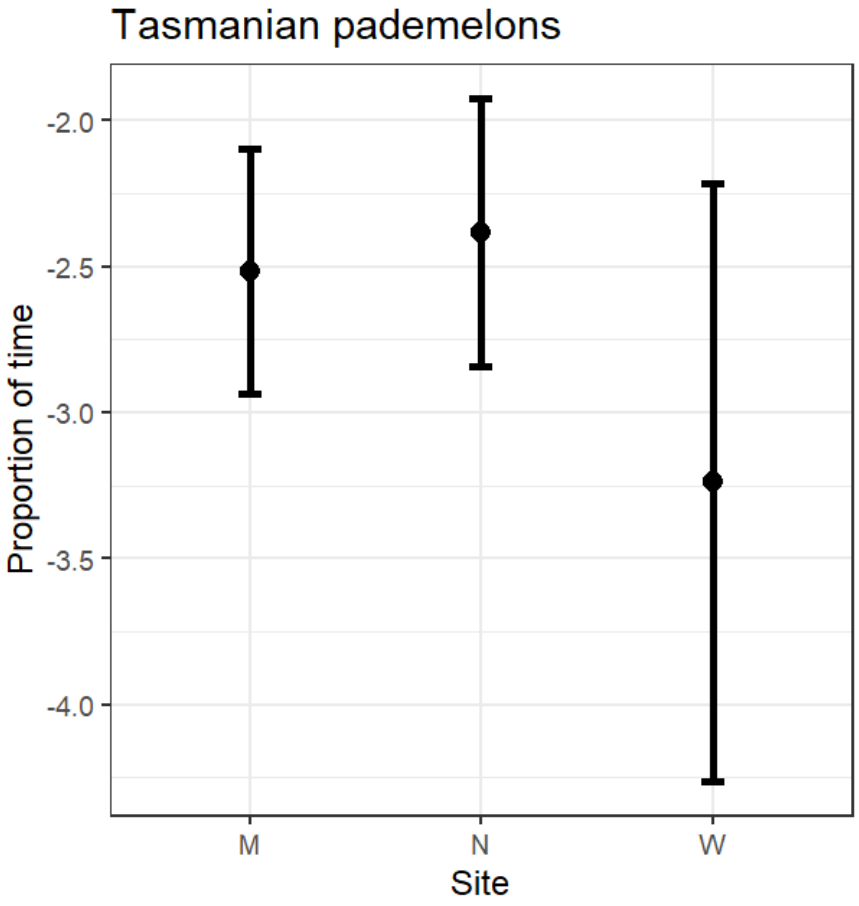

Figure 4.05:
Plot of the site effect on the proportion of time spent vigilant in Tasmanian pademelons observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.

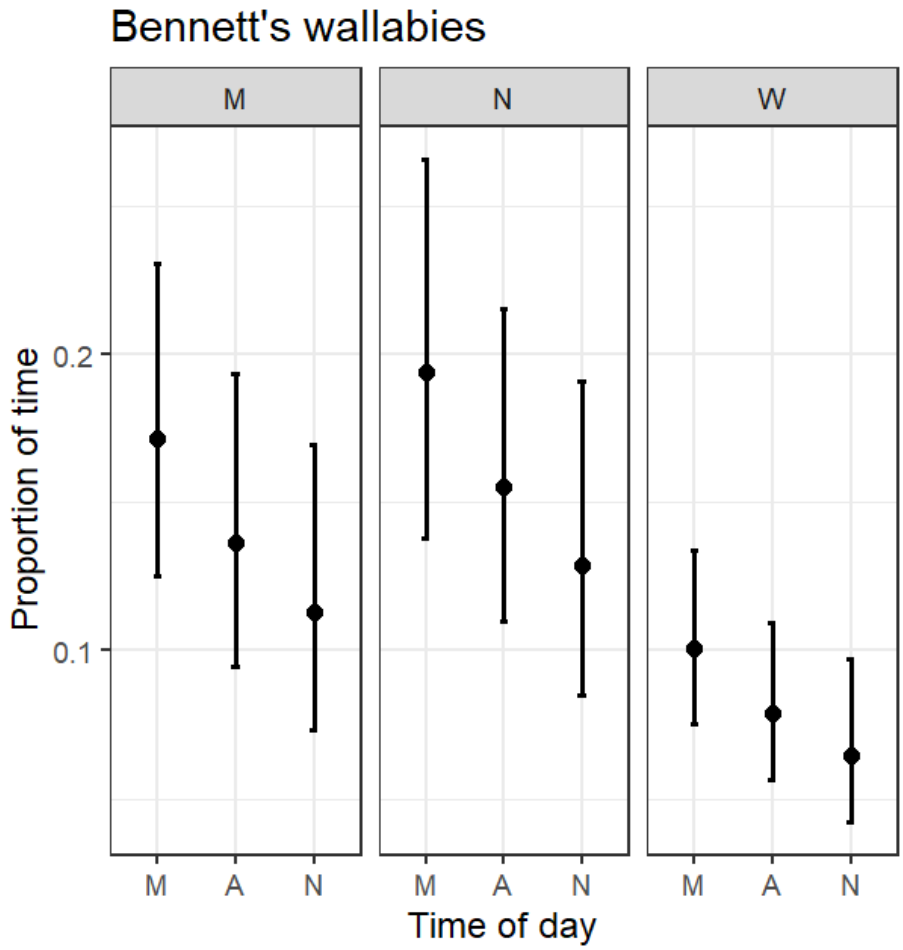

Figure 4.06: Plot of the site and time of day effect on the proportion of time spent vigilant in Bennett's wallabies observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019. Time of day: M= morning, A= afternoon, N= night.

Kangaroos: Vigilance behaviour was influenced by site, time of day and age. Greater vigilance scores were recorded in the morning than at night, and kangaroos were most vigilant at Narawntapu and least vigilant at Maria (Figure 4.07a and 4.07b). Subadult kangaroos showed slightly lower levels of vigilance than adults across all sites and both observers (expect during the afternoon, both ages showed similar levels of vigilant behaviour). The top model was multivariate, involving site and the interaction between age and time of day (Table 4.02). It carried 65% of the total model weight. The second (21% total ΔAIC model weight), third (8%) and fourth (4%) models, all involving the 'distance from cover' parameter, also had some influence on the response variable as they all had <6 ΔAIC units from the top model (Richards, 2008).Site and age were the most important variables according to the relative importance of variables, with RIV values of 0.975 and 0.777 respectively.

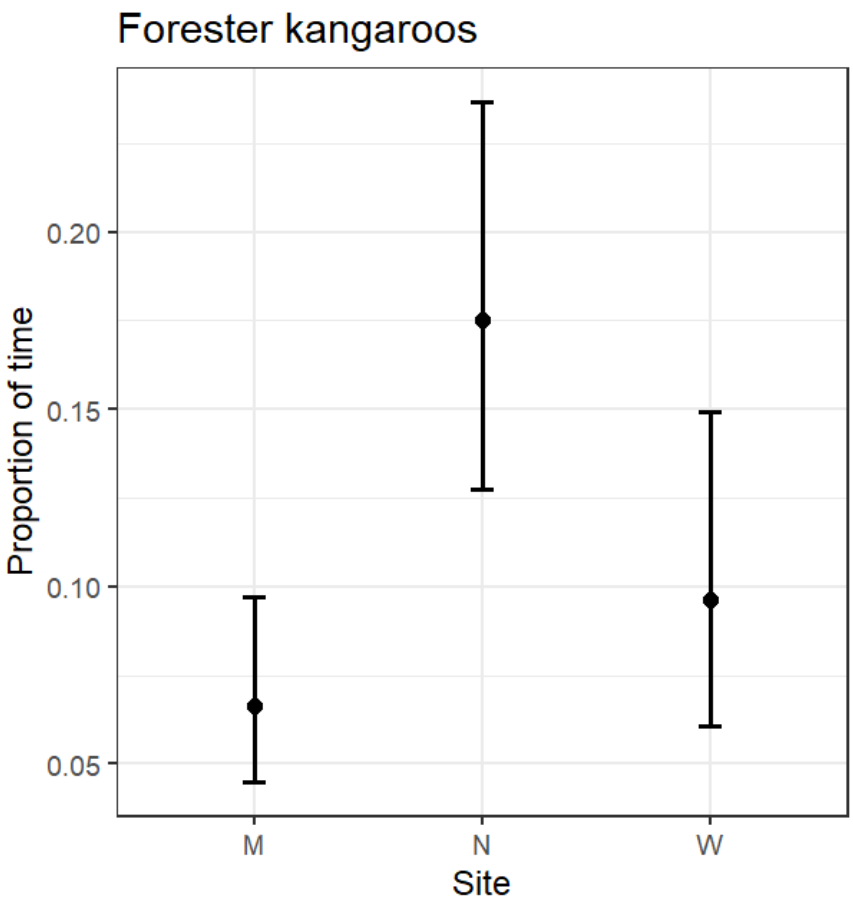

Figure 4.07a:
Plot of the site effect on the proportion of time spent vigilant in Forester kangaroos observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.

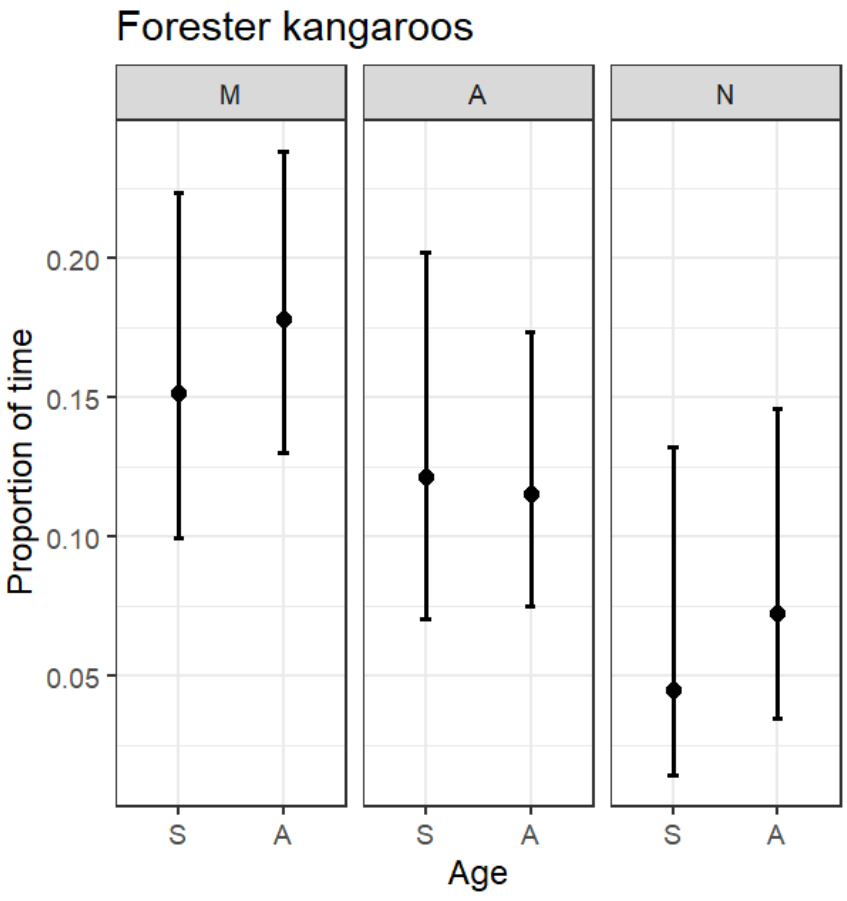

Figure 4.07b:
Plot of the interactive effects of age and time of day on the proportion of time spent vigilant in Forester kangaroos observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.

Model	Inter-cept	S	T	A	D	A*S	A*D	A*T	AIC	∆ AIC	AIC Weight
PADEMELON											
null	-2.529	—	—	—	—	—	—	—	680.4	0.00	0.369
A	-2.293	—		-0.344 ± 0.323	—	—	—	—	681.2	0.87	0.239
S	-2.518	0.134 ± 0.313	—	—	—	—	—	—	682.2	1.77	0.152
T	-2.351	—	-0.069 ± 0.403	—	—	—	—	—	683.2	2.79	0.091
S+A	-2.325	0.119 ± 0.312	—	-0.280 ± 0.321	—	—	—	—	683.4	3.02	0.082
S+T	-2.336	0.314 ± 0.350	-0.151 ± 0.425	—	—	—	—	—	684.2	3.86	0.053
S*A	-2.306	0.026 ± 0.532	—	-0.306 ± 0.454	—	0.146 ± 0.657	—	—	686.9	6.52	0.014
RI		0.301	0.144	0.335	0.000	0.014	0.000	0.000			
WALLABY											
S+T	-1.573	0.150 ± 0.239	-0.270 ± 0.203	—	—	—	—	—	1477.3	0.00	0.692
S+A+T	-1.666	0.143 ± 0.239	-0.269 ± 0.203	0.125 ± 0.212	—	—	—	—	1479.0	1.66	0.302
null	-2.005	—	—	—	—	—	—	—	1486.8	9.48	0.006
RI		0.994	0.994	0.302	0.000	0.000	0.000	0.000			
KANGAROO											
S+A*T	-2.224	1.097 ± 0.259	-0.255 ± 0.392	0.193 ± 0.307	—	—	—	-0.253 ± 0.488	1079.8	0.00	0.646
S+D	-2.398	1.011 ± 0.265	—	—	0.073 ± 0.239	—	—	—	1082.1	2.29	0.206
S+A+D	-2.454	1.008 ± 0.265	—	0.098 ± 0.234	0.068 ± 0.239	—	—	—	1084.0	4.12	0.082
S+A*D	-2.561	1.012 ± 0.265	—	0.266 ± 0.387	0.333 ± 0.387	—	-0.413 ± 0.476	—	1085.2	5.37	0.044
A+T	-1.771	—	-0.128± 0.249	0.138 ± 0.238	—	—	—	—	1089.7	9.91	0.005
T+D	-1.648	—	-0.123 ± 0.250	—	-0.094 ± 0.234	—	—	—	1089.9	10.08	0.004
null	-1.845	—	—	—	—	—	—	—	1090.5	10.66	0.003
RIV		0.978	0.655	0.777	0.332	0.000	0.044	0.646			

Table 4.02:
Final model set from GLMM of vigilance behaviour of Tasmanian pademelons, Bennett's wallabies and Forester kangaroos observed in 2019 at Maria Island, Narawntapu and wukalina/Mt William National Parks, Tasmania, Australia.
Model parameters:
S= site, T= time of day,
A= age,
D= distance from cover.
Parameter estimates ± Standard Error (SE) are included for each parameter in every model.

4.2 Flight Initiation Distance

Comparative analyses of 2001 and 2019 data sets

Pademelons: FID measurements were only influenced by observer. In 2019, pademelons had shorter flight initiation distances than in 2001 (difference between 2019 and 2001 = 1.05 ± 0.12). There were no other parameter influences of FID. The univariate model with the observer parameter carried the total AIC model weight (Table 4.03).

Wallabies: Wallabies showed a reduction in FID distance in 2019 compared to the data collected in 2002. There was also a site influence, where wallabies at wukalina had greater FID than those at Narawntapu (Figure 4.08). The model involving the site and observer parameters was the top model, with 72% of the total AIC model weight (Table 4.03). The second model, the interaction between site and observer, holds 28% of the total AIC model weight and had an ΔAIC value <2. These two parameters, comprising both of the top models, both have a RIV = 1, have great influence on the flight initiation distance of wallabies. All other models have ΔAIC units >6.

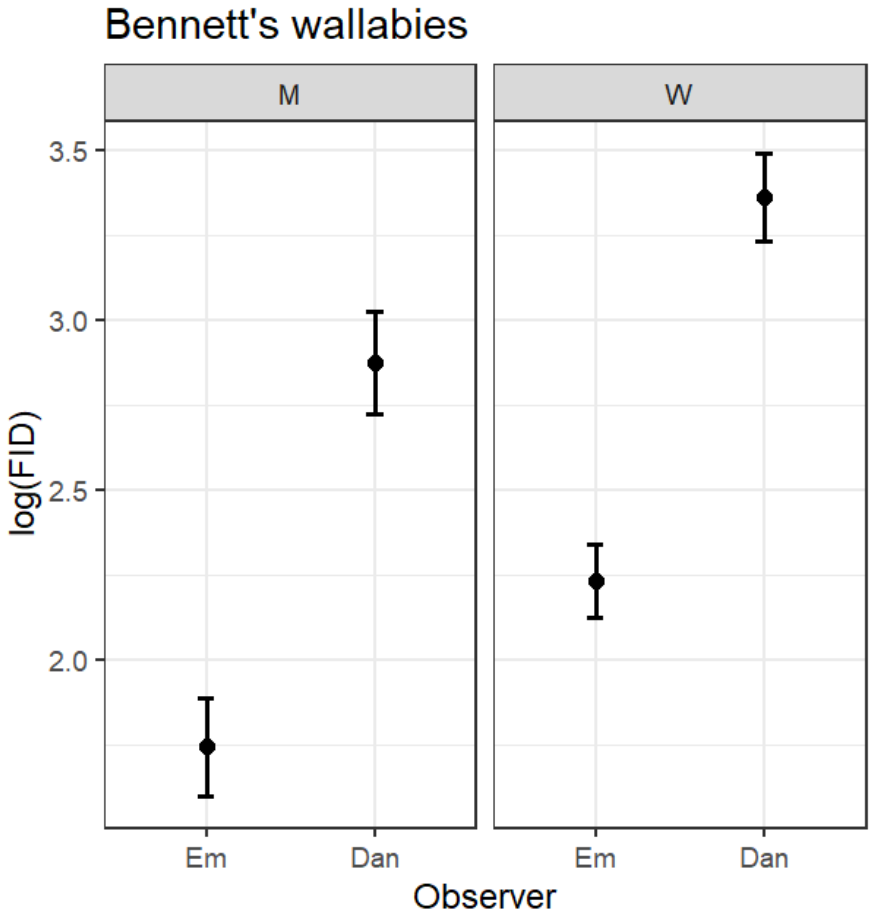

Figure 4.08: Plot of the site and observer effects on the flight initiation distance of Bennett's wallabies observed at Maria Island (M) and wukalina/Mt William (W) National Parks in 2019 (Emilie Roure) and 2009 (Daniel Blumstein).

Kangaroos: FID was influenced by observer and was lower in 2019 compared to 2001, although site also has a strong influence, with kangaroos at wukalina having much greater FIDs than kangaroos at Maria (Figure 4.09). The top model, a multivariate model with site and observer parameters, carried 72% of the total AIC model weight (Table 4.03). Similar to wallabies, kangaroos at wukalina national park show much greater FID than kangaroos at Narawntapu and Maria Island (no major differences between Maria Island and Narawntapu) (Figure 4.09). Similar to the AIC ranking of Bennett's wallabies, the interaction model between site and observer, holds 28% of the model weight and has a ΔAIC value of less than 2. This shows that site and observer, both with RIV = 1, had great influence on the flight initiation distance of wallabies. All other models had little influence on the response variable with ΔAIC units >6 (Richards, 2008).

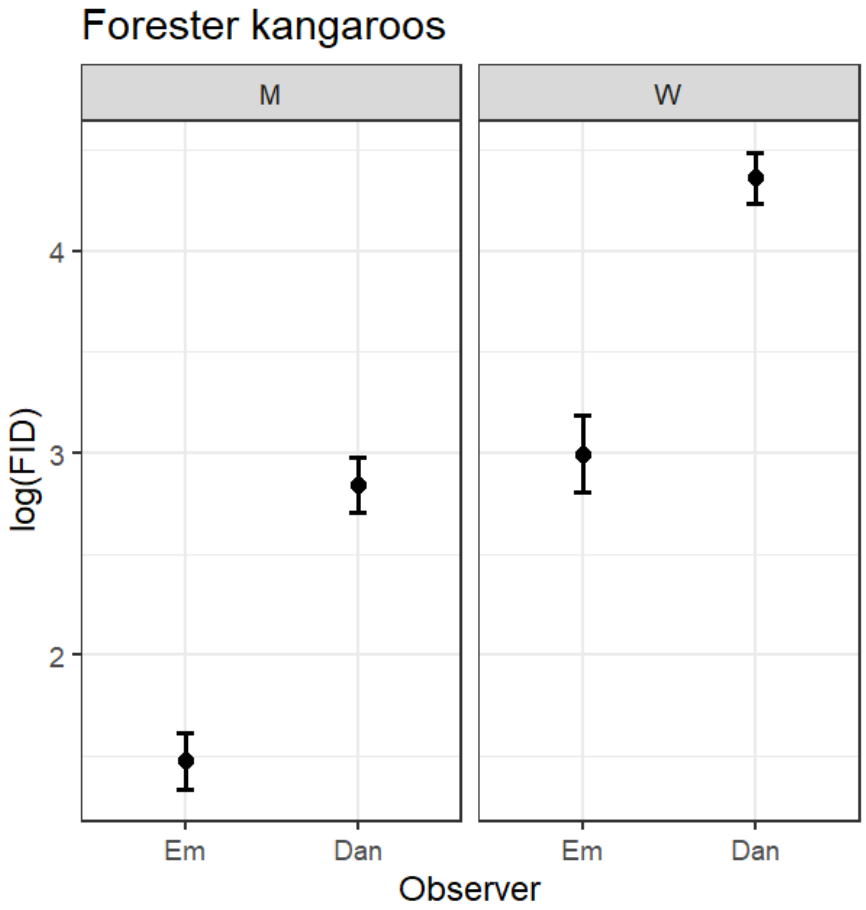

Figure 4.09: Plot of the site and observer effects on the flight initiation distance of Forester kangaroos observed at Maria Island (M) and wukalina/Mt William (W) National Parks in 2019 (Emilie Roure) and 2009 (Daniel Blumstein).

Table 4.03: Final model set from GLMM of flight initiation distances of Tasmanian pademelons (Narawntapu National Park), Bennett's wallabies and Forester kangaroos (Maria Island and wukalina/Mt William National Parks) observed in 2001 and 2019 in Tasmania, Australia.
Model parameters: O= observer, S= site, T= time of day, D= distance from cover.
Parameter estimates ± Standard Error (SE) are included for each parameter in every model.

Model	Inter-cept	O	S	T	D	O*S	S*T	O*T	S*D	AIC	∆ AIC	AIC Weight
PADEMELON												
O	1.779	1.045 ± 0.115	—	—	—	—	—	—	—	274.2	0.000	1
null	2.425	—	—	—	—	—	—	—	—	337.3	63.05	0
RIV		1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
WALLABY												
S+O	1.743	1.129 ±0.077	0.489 ± 0.080	—	—	—	—	—	—	553.1	0.00	0.722
S*O	1.757	1.098 ± 0.130	0.469 ± 0.106	—	—	0.048 ± 0.161	—	—	—	555.0	1.91	0.278
O + T	2.040	1.089 ± 0.089	—	0.077 ± 0.089	—	—	—	—	—	589.8	36.76	0.000
O*T	2.070	0.940 ± 0.173	—	0.023 ± 0.104	—	—	—	0.202 ± 0.202	—	590.8	37.74	0.000
S+T	2.026	—	0.372 ± 0.102	0.326 ± 0.105	—	—	—	—	—	698.7	145.64	0.000
S*T	2.084	—	0.280 ± 0.173	0.235 ± 0.176	—	—	0.141 ± 0.219	—	—	702.2	149.19	0.000
null	2.523	—	—	—	—	—	—	—	—	725.6	172.56	0.000
RIV		1.000	1.000	0.000	0.000	0.278	0.000	0.000	0.000			
KANGAROO												
S+O	1.476	1.368 ± 0.090	1.518 ± 0.087	—	—	—	—	—	—	428.4	0.00	0.724
S*O	1.468	1.384 ± 0.108	1.556 ± 0.168	—	—	-0.053 ± 0.197	—	—	—	430.3	1.93	0.276
S+D	1.844	—	2.072 ± 0.124	—	0.420 ± 0.127	—	—	—	—	545.8	117.42	0.000
S*D	1.938	—	1.910 ± 0.199	—	0.291 ± 0.177	—	—	—	0.265 ± 0.254	546.7	118.31	0.000
O+D	1.959	1.96 ± 0.132	—	—	-0.285 ± 0.133	—	—	—	—	574.3	145.93	0.000
null	3.011	—	—	—	—	—	—	—	—	765.8	337.39	0.000
RIV		1.000	1.000	0.000	0.000	0.276	0.000	0.000	0.000			

Analysis of 2019 dataset

Pademelons: FID distances were greatly influenced by site, with greater distances at Narawntapu than at Maria. Time of day was also influential as pademelons in the morning were much flightier than those in the afternoon or night (Figure 4.10). This is reflected in the top model of the AIC table, the interaction term between site and time of day which carried 94% of the total AIC model weight (Table 4.04). Overall, adults also had greater FIDs than subadult individuals. However, only the top model had influence on the response variable. The relative importance of variables showed that site (RIV = 1) and time of day (RIV = 1) were the most influential parameters for pademelon FIDs.

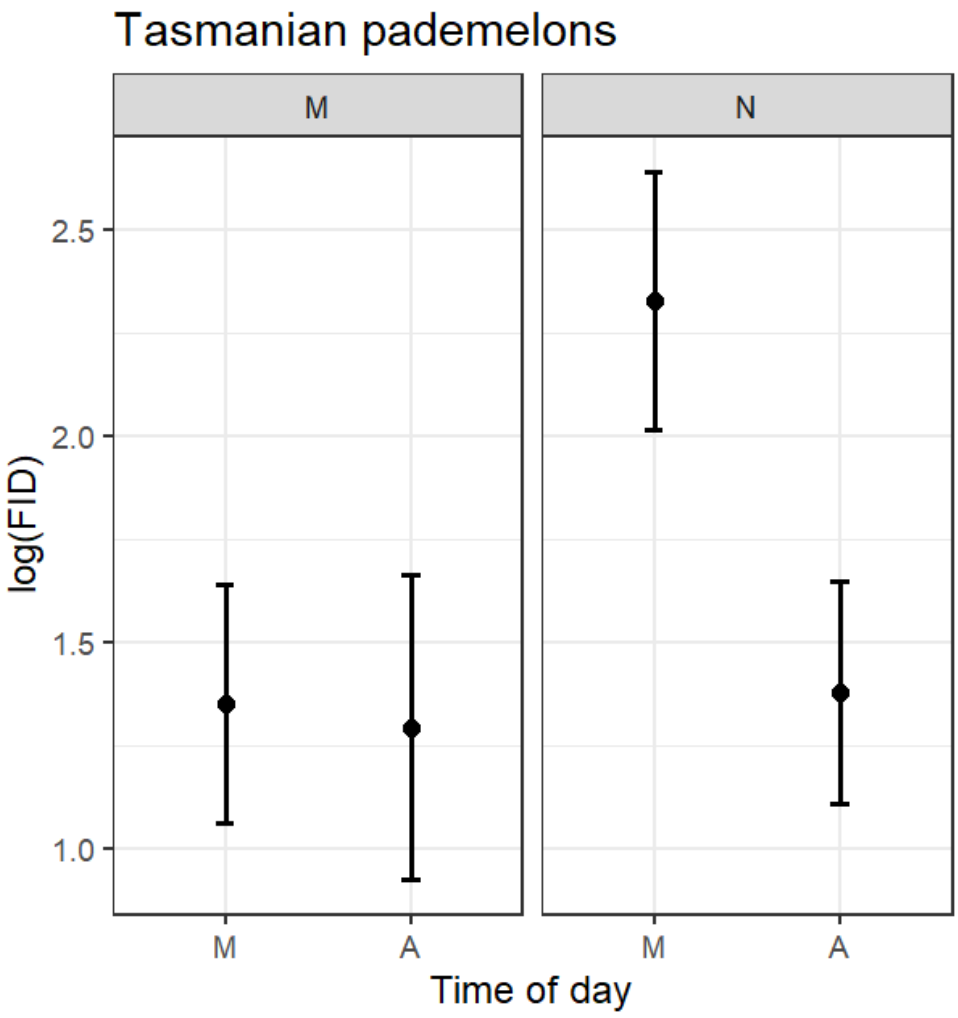

Figure 4.10: Plot of the interactive effects of site and time of day (M= morning, A= afternoon) on the flight initiation distance of Tasmanian pademelons observed at Maria Island (M) and Narawntapu (N) National Parks in 2019.

Wallabies: FID was greatly influenced by the site parameter, with the greatest FIDs seen in wallabies at wukalina (Figure 4.11). Time of day also had some influence, as wallabies observed in the morning had shorter FIDs than those observed in the afternoon. The top-ranking model was a univariate model involving site exclusively and carried 37% of the total AIC model weight (Table 4.04). All models, excluding the null model, had some influence on wallaby FID, with ΔAIC units <6 from the top model (Burnham et al., 2011a). These models all included the site parameter (RIV = 1), which showed that it was the most important parameter influencing the FID of wallabies in the data collected in 2019.The relative importance of variables showed that age (RIV = 0.317) and time of day (0.448) also had some influence on the FIDs.

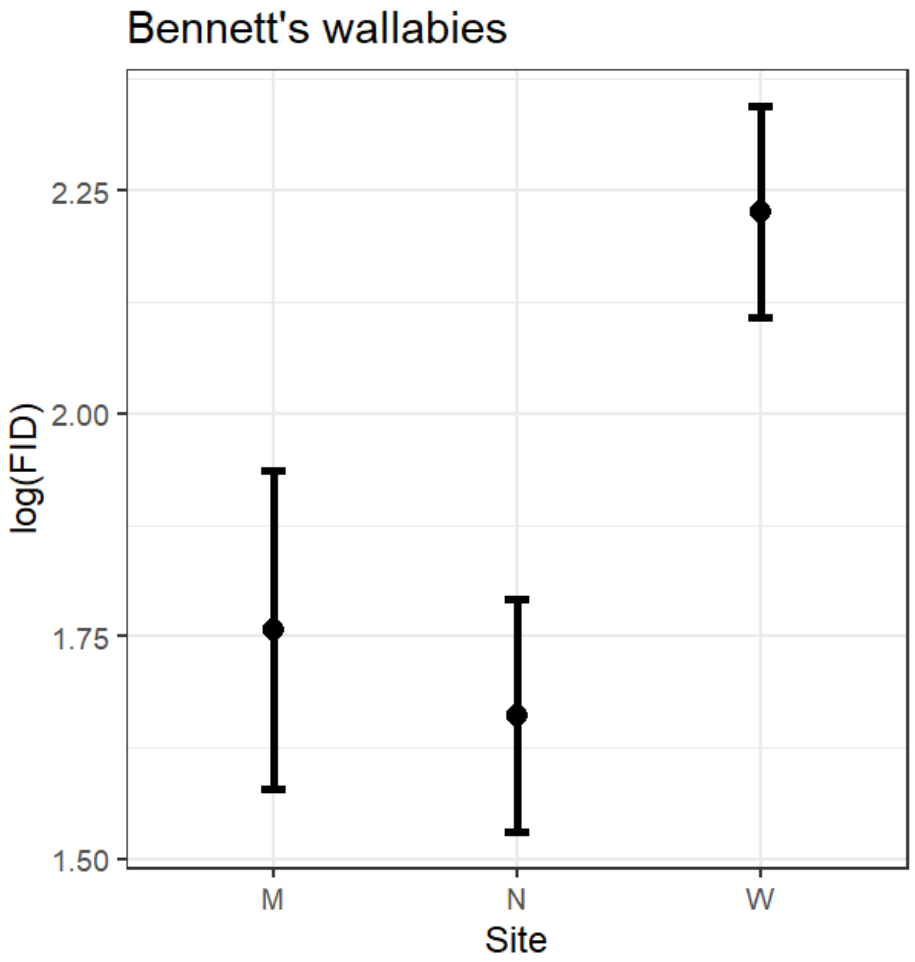

Figure 4.11: Plot of site effect on the flight initiation distance of Bennett's wallabies observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.

Kangaroos: FID was most influenced by site differences and the greatest FIDs were seen at wukalina, the lowest at Maria. Distance from cover also had some influence as kangaroos >30m away from cover had greater FIDs than kangaroos closer to cover. Subadult individuals also showed slightly greater FIDs than adults, across all three sites (Figure 4.12). The multivariate model involving site and distance from cover ranked as the top model and carried 52% of the total AIC model weight (Table 4.04). The second model (24% total AIC weight), a multivariate model involving site, distance from cover and age, was less than 2 ΔAIC units from the top model therefore having a high influence on FID. All models which have influence (<6 ΔAIC units from the top model) on wallaby FID involve the site parameter. The relative importance of variables showed that the order of importance of these parameters was site (RIV = 1), distance from cover (RIV = 0.853), and age (0.395).

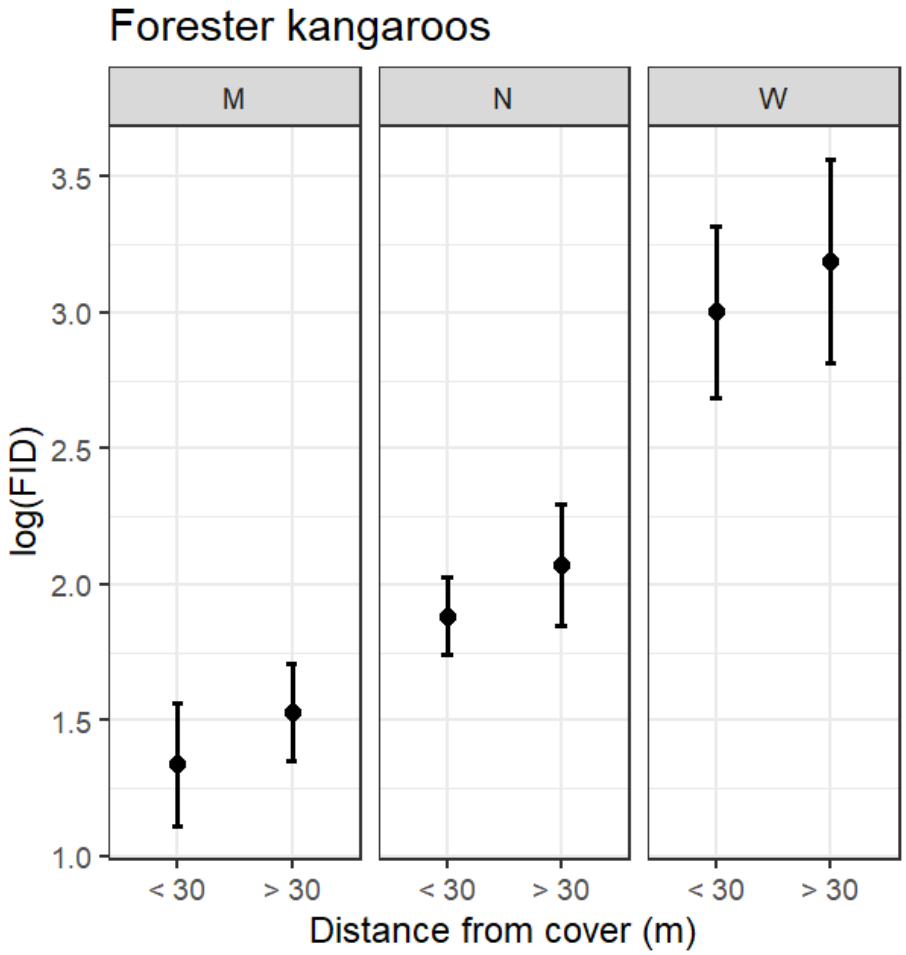

Figure 4.12: Plot of site and distance from cover effects on the flight initiation distance of Forester kangaroos observed at Maria Island (M), Narawntapu (N) and wukalina/Mt William (W) National Parks in 2019.

Model	Inter-cept	S	T	A	D	S*T	S*A	T*A	D*A	AIC	∆ AIC	AIC Weight
PADEMELON												
S*T	1.350	0.978 ± 0.218	-0.056 ± 0.239	—	—	-0.894 ± 0.319	—	—	—	219.0	0.00	0.937
S+T+A	1.402	0.567 ± 0.165	-0.553 ± 0.164	0.192 ± 0.174	—	—	—	—	—	225.6	6.62	0.034
S+T*A	1.556	0.564 ± 0.164	-0.847 ± 0.290	-0.023 ± 0.247	—	—	—	0.426 ± 0.347	—	226.1	7.04	0.028
S*A	1.047	0.685 ± 0.310	—	0.394 ± 0.281	—	—	-0.323 ± 0.372	—	—	236.0	17.03	0.000
null	1.578	—	—	—	—	—	—	—	—	239.0	20.01	0.000
D+A	1.448	—	—	0.167 ± 0.190	0.651 ± 0.610	—	—	—	—	240.9	21.85	0.000
RIV		1.000	1.000	0.062	0.000	0.937	0.000	0.028	0.000			
WALLABY												
S	1.757	-0.096 ± 0.113	—	—	—	—	—	—	—	541.2	0.00	0.369
S+T	1.797	-0.067 ± 0.117	-0.082 ± 0.089	—	—	—	—	—	—	542.3	1.13	0.210
S*A	1.662	-0.030 ± 0.185	—	0.155 ± 0.187	—		-0.111 ± 0.233	—	—	542.6	1.40	0.184
S*T	1.838	0.057 ± 0.256	-0.168 ± 0.182	—	—	-0.112 ± 0.256	—	—	—	543.7	2.52	0.105
S+T+A	1.832	-0.065 ± 0.117	-0.083 ± 0.089	-0.058 ± 0.086	—	—	—	—	—	543.9	2.68	0.097
S+T*A	1.817	-0.065 ± 0.118	-0.058 ± 0.152	-0.033 ± 0.150	—	—	—	-0.036 ± 0.184	—	545.8	4.64	0.036
null	1.928	—	—	—	—	—	—	—	—	578.2	37.04	0.000
RIV		1.000	0.448	0.317	0.000	0.105	0.184	0.036	0.000			
KANGAROO												
S+D	1.339	0.545 ± 0.121	—	—	0.189 ± 0.118	—	—	—	—	356.6	0.00	0.523
S+D+A	1.374	0.551 ± 0.121	—	-0.069 ± 0.104	0.195 ± 0.118	—	—	—	—	358.2	1.55	0.241
S+D*A	1.371	0.551 ± 0.121	—	-0.064 ± 0.131	0.203 ± 0.179	—	—	—	-0.013 ± 0.215	360.2	3.55	0.089
S+T	1.511	0.487 ± -0.088	-0.088 ± 0.116	—	—	—	—	—	—	360.3	3.71	0.082
S+T+A	1.572	0.501 ± 0.120	-0.113 ± 0.120	-0.087 ± 0.108	—	—	—	—	—	361.7	5.04	0.042
S+T*A	1.461	0.503 ± 0.120	0.029 ± 0.202	0.059 ± 0.199	—	—	—	-0.206 ± 0.236	—	362.9	6.25	0.023
null	1.868	—	—	—	—	—	—	—	—	416.3	59.69	0.000
T+D	1.970	—	-0.034 ± 0.128	—	-0.201 ± 0.126	—	—	—	—	418.8	62.17	0.000
RIV		1.000	0.147	0.395	0.853	0.000	0.000	0.023	0.089			

Table 4.04: Final model set from GLMM of flight initiation distances of Tasmanian pademelons, Bennett's wallabies and Forester kangaroos observed in 2019 at Maria Island, Narawntapu and wukalina/Mt William National Parks, Tasmania, Australia. Model parameters: S= site, T= time of day, A= age, D= distance from cover. Parameter estimates ± Standard Error (SE) are included for each parameter in every model.

4.3 Emergence time and distance from cover

Comparative analyses of 2009 and 2019 data sets - Emergence time from cover

Pademelons: At all sites in 2019, pademelons were present in low numbers during before-dusk (BD) and dusk (D) timeslots, especially when compared to the two other study species (Appendix D). They also emerged from cover later in the day in 2019 compared to 2009, however, there were greater numbers of pademelons seen on transects in 2009 than in 2019. There was some site influence, with the greatest abundance of pademelons on transects at Narawntapu for both observers/years.

Wallabies: Fewer wallabies were present on transects in 2019 compared to 2009. At all sites they were found in similar numbers during dusk, night and midnight in 2019. During the before-dusk timeslot in 2019, the lowest number of wallabies were seen at Maria than at the other two sites, with the greatest at wukalina (Appendix D). During the 2009 dataset at Narawntapu, there was a peak in wallaby numbers during the dusk timeslot. The greatest abundance of wallabies on transects was seen at wukalina for both 2009 and 2019.

Kangaroos: Kangaroos greatly increased in numbers on transects from 2009 to 2019. For both data sets, there was the greatest abundance of kangaroos present on transects during the before dusk timeslot (Appendix D). At wukalina in 2019, there were few kangaroos present on transects overall, with only 21 kangaroos spotted on transects in total. The greatest numbers of kangaroos on transects were at Maria in both 2009 and 2019.

Comparative analyses of 2009 and 2019 data sets - Emergence distance from cover

Pademelons: Emergence distance was strongly influenced by time of day (timeslot), and there was an obvious peak in their emergence distance at night. Emergence distances in pademelons were also influenced by site and age, where the greatest distances from cover were documented at Narawntapu and the shortest at Maria (Figure 4.13). Adults emerged to greater distances from cover, the edge of the forest, than subadults. The top model included all three of these parameters, site, age and time of day and carried 99% of the total AIC model weight (Table 4.05). The second model, which included site, observer and time of day, carried 1% of the total model weight and did not have any had influence on the response variable with a ΔAIC value >6 (Richards, 2008). The most influential parameters, site and time of day had a RIV = 1, and age had a RIV = 0.989.

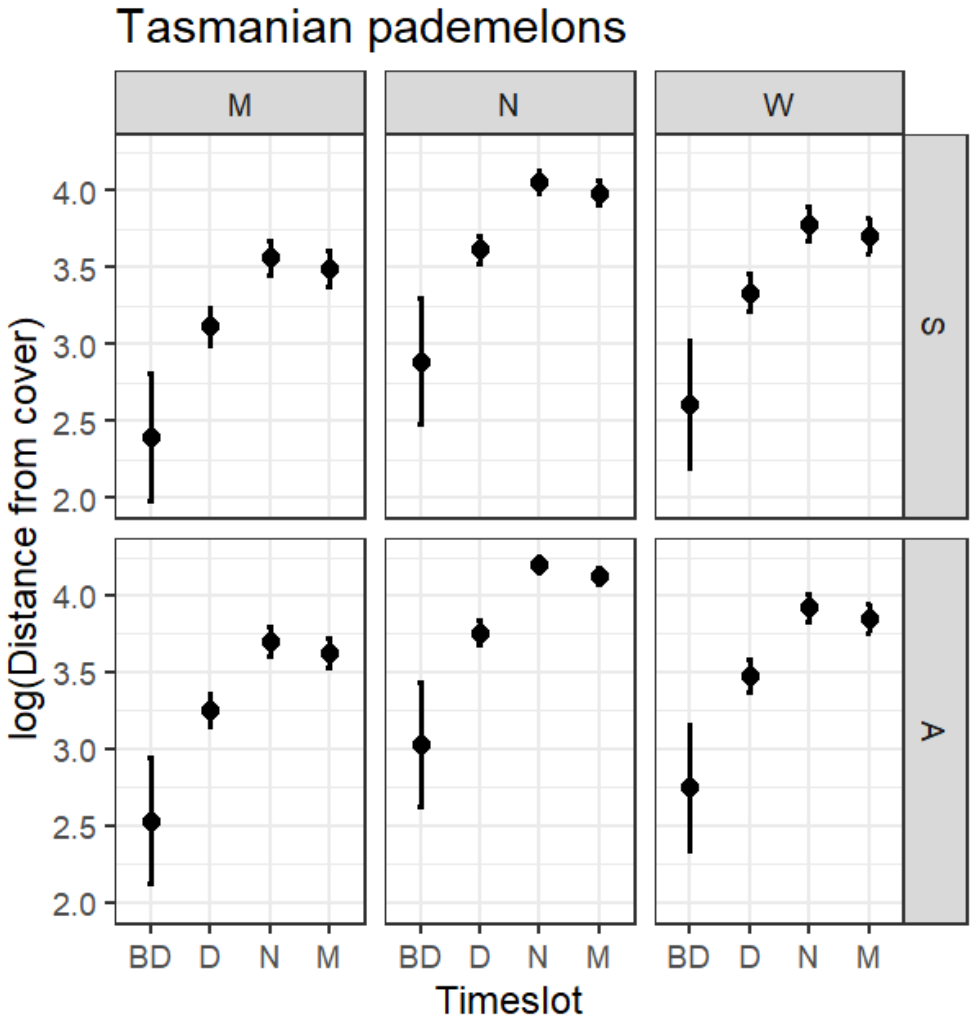

Figure 4.13: Site, age and time of day influence on the emergence from cover distance of Tasmanian pademelons observed at Maria Island, Narawntapu and wukalina/Mt William National Parks in 2009 and 2019. Time of day: BD = before dusk, D = dusk, N = night, M = midnight;
Age: S = subadult, A= adult

Wallabies: Emergence distances of wallabies, like pademelons, were influenced by site, age and time of day. At all sites, subadult individuals foraged at closer distances to cover. Both adults and subadults emerged the furthest from cover during the night and were closest to cover before dusk. The greatest emergence distances were at wukalina and the shortest at Maria (Figure 4.14). The top model included three variables: site, age and time of day, and carried 95% of the total AIC model weight (Table 4.05). The second model only carried 5% of the total AIC model weight an did not have influence (ΔAIC value >6 (Richards, 2008). It included site, observer and time of day. Time of day and site were of high influence on wallaby emergence distances, with RIV scores of 1 (age RIV = 0.954).

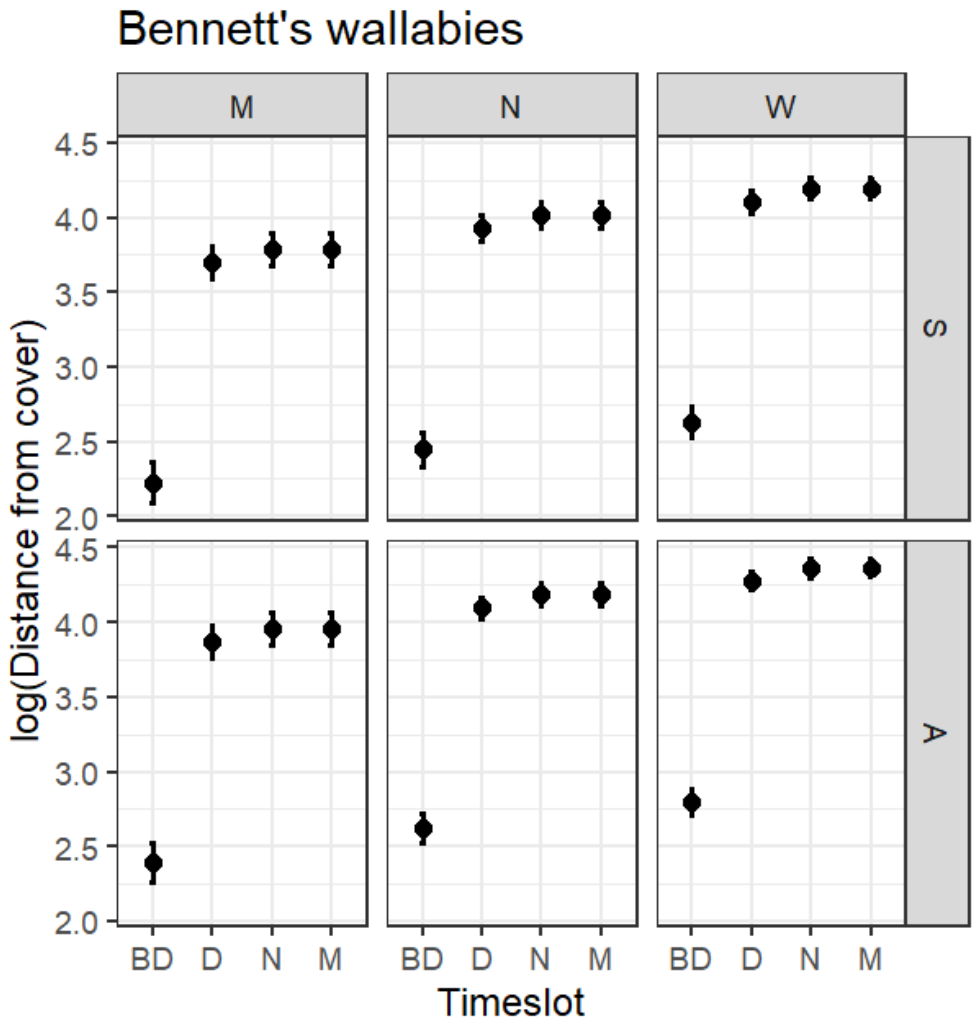

Figure 4.14: Site, age and time of day influence on the emergence from cover distance of Bennett's wallabies observed at Maria Island, Narawntapu and wukalina/Mt William National Parks in 2009 and 2019. Time of day: BD = before dusk, D = dusk, N = night, M = midnight;
Age: S = subadult, A= adult

Kangaroos: Emergence distances of kangaroos were greatly influenced by site, observer and time of day parameters. Across all sites, kangaroos observed before dusk had the shortest emergence distances from cover, and those observed at night had the greatest distances from cover (Figure 4.15). Kangaroos observed in 2019 emerged a greater distance from cover than kangaroos in 2009. For both observers, kangaroos on Maria had the shortest emergence distances whereas those at wukalina emerged the furthest from cover (Figure 4.15). The multivariate model with the site, observer and time of day parameters was the top-ranking model and carried 93% of the total AIC model weight (Table 4.05). The second model, a multivariate model with site and observer and an interaction term between age and time of day, carried 6% of the total AIC model weight. The other models had no influence on emergence distances as they have ΔAIC values >6 from the top model. The relative importance of variables further indicated that time of day (RIV = 1) was the most influential parameter, followed by the site parameter (RIV = 0.998) and observer (RIV = 0.990).

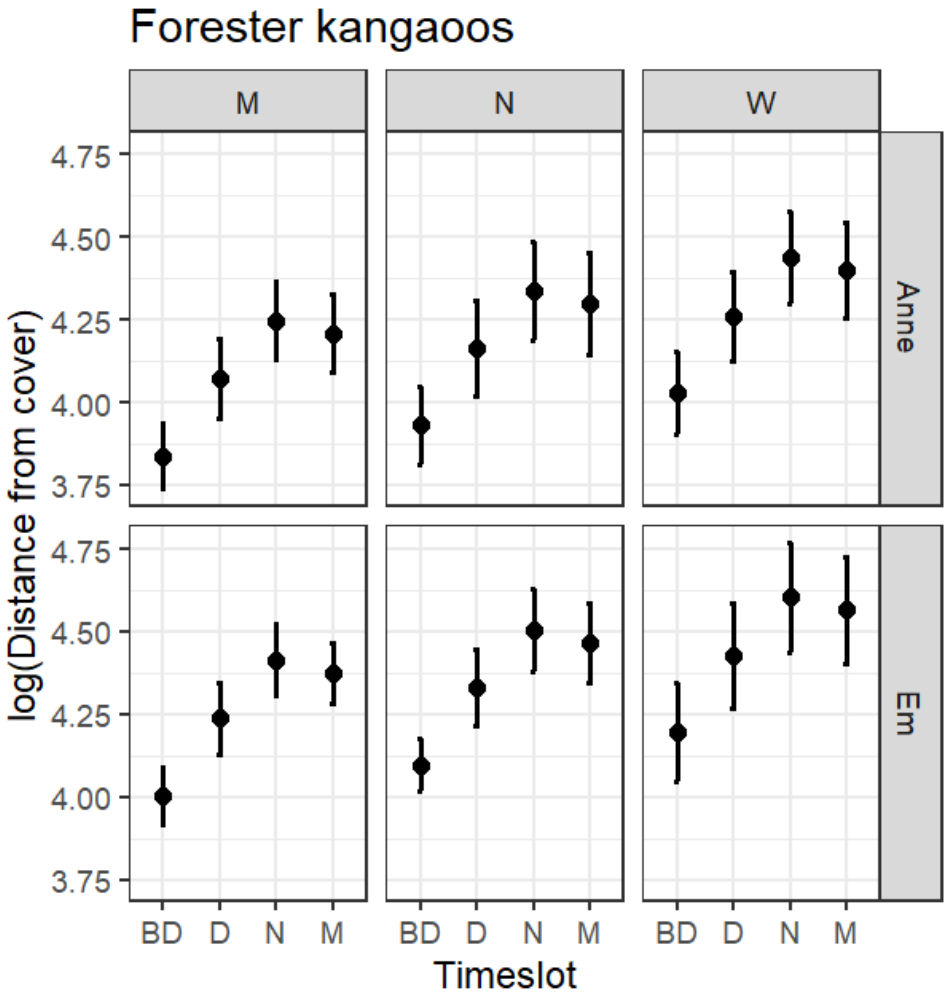

Figure 4.15: Site, observer and time of day influence on the emergence from cover distance of Forester kangaroos observed at Maria Island, Narawntapu and wukalina/Mt William National Parks in 2009 (Anne Nielsen) and 2019 (Emilie Roure).
Time of day: BD = before dusk, D = dusk, N = night, M = midnight.

Table 4.05: Final model set from GLMM of emergence distance of Tasmanian pademelons, Bennett's wallabies and Forester kangaroos observed in 2009 and 2019 at Maria Island, Narawntapu and wukalina/Mt William National Parks, Tasmania, Australia. Model parameters: O= observer, S= site, T= time of day, A= age.
Parameter estimates ± Standard Error (SE) are included for each parameter in every model.

Model	Inter-cept	O	S	T	A	S*A	AIC	∆ AIC	AIC Weight
PADEMELON									
S+A+T	2.391	—	0.499 ± 0.049	0.726 ± 0.210	0.141 ± 0.038	—	8497.4	0.00	0.989
S+O+T	2.554	-0.075 ± 0.035	0.482 ± 0.049	0.680 ± 0.210	—	—	8506.4	8.99	0.011
null	3.953	—	—	—	—	—	8755.7	258.30	0.000
RIV		0.011	1.000	1.000	0.989	0.000			
WALLABY									
S+A+T	2.223	—	0.227 ± 0.058	1.477 ± 0.051	0.169 ± 0.034	—	6718.5	0.00	0.954
S+O+T	2.386	-0.136 ± 0.032	0.029 ± 0.058	1.452 ± 0.051	—	—	6724.5	6.06	0.046
null	4.019	—	—	—	—	—	7654.9	936.43	0.000
RIV		0.046	1.000	1.000	0.954	0.000			
KANGAROO									
S+O+T	3.838	0.167 ± 0.050	0.092 ± 0.050	0.232 ± 0.058	—	—	2657.7	0.00	0.928
S+O+A*T	3.793	0.168 ± 0.050	0.091 ± 0.050	0.282 ± 0.113	0.062 ± 0.071	-0.067 ± 0.131	2663.2	5.43	0.062
S+A+T	3.902		0.131 ± 0.049	0.233 ± 0.058	0.059 ± 0.048	—	2667.3	9.52	0.008
T	4.016	—	—	0.217 ± 0.058	—	—	2670.7	13.00	0.001
A+T	3.972	—	—	0.217 ± 0.058	0.060 ± 0.048	—	2671.2	13.45	0.001
null	4.193	—	—	—	—	—	2724.3	66.55	0.000
RIV		0.990	0.998	1.000	0.071	0.062			

5. **Discussion**

The key results of the study are that species ecology, body size and age of the prey animal, and environmental factors, such as changes in vegetation structure, strongly influence the expression of risk-sensitive behaviours in macropods. I did not find universal responses in all three macropod species to the change in devil abundance. At wukalina/Mt William National Park, although devil abundance had not changed over time, the behaviour of macropods showed an increase in the perceived risk of predation with increased vigilance in wallabies and overall greater FIDs for all three species than at the other two sites. These behaviours may relate to the natural regrowth of vegetation in this National Park that was previously cleared for farming. At Narawntapu National Park, which had a dramatic reduction in devil abundance between the two study timeframes, risk-sensitive behaviours of the macropods did not change and continued to be greater (greatest proportion of time spent vigilant of all sites in all species in 2019) than at Maria Island National Park, where devils were introduced. Macropods at Maria Island National Park did not show any major trends of increases in antipredator behaviour following the introduction and increase in population density of devils to carrying capacity. Independent of changing devil abundance, time of day significantly influenced macropod behaviour, with macropods observed in the morning being most vigilant, and those at night least vigilant. The behaviour of subadult macropods indicated a greater perceived level of risk than adults, with higher vigilance scores, greater FID and shorter emergence distances from cover. These results indicate that changes in abundance of the top terrestrial predator in Tasmanian ecosystems, the Tasmanian devil, does not translate into changes in the three measured risk-sensitive behaviours in macropods, including their major prey species. Rather, the body-size and ecology of the prey species may interact with and limit the effects of changing predator abundance on prey behaviour.

The three risk-sensitive behaviours of focus for this research represent three different mechanisms for predator avoidance. None of the antipredator behaviours observed showed evidence of being influenced by predator presence across all three species. Animals with a greater perceived level of threat will assess their surroundings more and have greater vigilance scores (Brown et al., 2014). Of all three study species, wallabies were the only species to show an increase in vigilance behaviour over time. This increase in behaviour was observed only at wukalina/Mt William National Park, which has had no devil increase over time, suggesting that this behaviour was not in response to predator pressure but to vegetation regrowth. Vegetation regrowth may decrease the chance of wallabies detecting an approaching devil in sufficient time to respond and evade detection or capture. Kangaroos may be less sensitive to vegetation regrowth because they forage well into in the

open and will be less impacted to these subtle changes in ecosystem structure (Banks, 2001). Pademelon may also not show an increase in vigilance because their smaller body size means they are highly susceptible to predators all the time, and maintain a constant highly-vigilant state (Rose and Rose, 2018, le Mar, 2002).

In many species, flight initiation distance (FID) directly reflects a prey animal's individual predator experience (Blumstein et al., 2003). Individuals with greater experience are more capable of distinguishing between lethal and non-lethal threats and will have shorter FIDs than individuals without experience. Smaller individuals, which are more susceptible to predation will have greater FIDs. This is reflected in the greater FIDs of smaller and younger individual macropods in this research.

Emergence time and distance from cover reflect behavioural decision-making and trade-offs between foraging and protection. In smaller species, more wary animals stay closer to cover, favouring the safety of vegetation over access to good forage, whereas in larger species, greater emergence from cover allows for early detection and rapid response to predators emerging from forest edges (While and McArthur, 2006, While and McArthur, 2005, Banks, 2001). My results show that emergence time and distance are most strongly influenced by ecological niche and body size, but also reflect experience (age). Emergence distances from cover were greater in larger individuals (larger species and adults within each species). The greatest emergence distances from cover were seen at wukalina/Mt William National Park for wallabies and kangaroos, where they are possibly responding to an increase in the perceived level of risk due to vegetation infringement. The latest emergence times were seen in smaller, browsing species that are most vulnerable to all predators, including diurnal raptorial predators.

While I was careful to exactly replicate the methods used by researchers in the two 'before' studies, the 'before-after' comparison is completely and unavoidably confounded with observer. Small methodological differences resulted in the exclusion of one data set for comparative analysis. I also found some effects which could not be explained by environmental change and could be due to observer effects (e.g. decreased FID for all species at all sites) although the method appears straightforward to implement.

In summary, the results of this study highlight the influence of an individual's (species) ecology, body-size and age, as well as time of day and vegetation structure. Study period (i.e. observer) may also make a difference to the results for some behaviours. Changes in the abundance of the top terrestrial predator, the Tasmanian devil, did not result in major changes in anti-predator behaviours in any of the three species of macropod.

Influence of body size, age and species ecology

Body size has a direct relationship with the vulnerability of prey species to predators in their environment (Werner and Gilliam, 1984, Periquet et al., 2012). The ecological niche and the level of threat which individuals experience will shape the type and variety of antipredator behaviours they express (Lingle and Pellis, 2002). Smaller-bodied prey species are susceptible to a larger number and size range of predators and will avoid interactions with a greater number of species in their environment (Fancourt, 2015). Pademelons are an example of a small species and are prey to devils, spotted-tailed quolls, feral cats, and eagles, including both wedgetail eagles and sea eagles (Andersen et al., 2017, Debus and Rose, 1999, Fuentes and Olsen, 2015, Debus, 2019). These predators are a range of nocturnal and diurnal, and mammalian and raptorial species, so pademelons are not safe from predation in the forest or in the open, day or night. Due to their greater susceptibility to predation, pademelons expressed more wary and vigilant behaviours than wallabies and kangaroos. (Blumstein and Daniel, 2003, Rudolf, 2012). Smaller arboreal prey species, brushtail possums, have shown flexibility in risk-sensitive behaviour in response to devil density changes in previous studies (Cunningham et al., 2019a, Hollings et al., 2015b). However, pademelon behaviour failed to indicate any influence of site or study period/observer on their behaviour, even at Maria Island National Park, where devil abundance had greatly increased over time. This suggests that pademelons may not show changes in risk-sensitive behaviour in response to changes in devil density as they maintain higher levels of antipredator behaviour, irrespective of environmental conditions, due to their high vulnerability to a wider range of predators in the ecosystem (Clancy, 1982).

Larger macropods, such as kangaroos, which are too big to rely on vegetation cover for protection commonly forage in groups (Colagross and Cockburn, 1993). Group foraging increases group size effects reducing the risk of predation and improving foraging rates (Blumstein et al., 2001, Coulson, 1993). Kangaroos are known to forage in large groups for protection and this was evident throughout the 2019 data collection period (Kaufmann, 1975). However, as group foraging was not seen in pademelons or wallabies, microhabitat use (related to species ecology) is also has an influence on the expression of this antipredator behaviour. Previous research in fish has shown that congregations of large and small individuals in a microhabitat increases the risk of predation for the smaller individuals (Rodgers et al., 2015, Colagross and Cockburn, 1993, Croft, 1989). Different microhabitat use between pademelon and kangaroo species was apparent in this research, with wallabies having some overlap in habitat use of both species. Wallabies showed an increase in vigilance behaviour at wukalina/Mt William National Park. They are intermediate between strategies of antipredator behaviour of kangaroos and pademelons being a major prey species to devils, less

vulnerable than pademelons but more vulnerable than kangaroos (While and McArthur, 2005). Wallabies feed out in the open unlike pademelons, but do not engage in group foraging behaviour (Blumstein and Daniel, 2003). These disparities in behaviour among macropods are influenced by niche and body size differences, but may also act in reducing predation risk by reducing the density of macropods in a specific microhabitat (Taylor, 1984, Ramp and Coulson, 2002).

Young individuals, both unweaned juvenile and weaned subadults, are not only smaller in body size, but also lack the life experience of living with predatory threats. They occupy sheltered microhabitats of the environment with adequate vegetation cover to avoid detection from predators (Jarman, 1984, Johnson and Bayliss, 1981). Avoiding detection by predators is more effective than fleeing from predators, especially for subadult prey which cannot move as fast as adults (Blumstein, 1998, Jarnemo et al., 2004). This behaviour is well illustrated by the subadult macropods in this study which had the highest vigilance scores, greatest FIDs and shortest emergence distances from cover at all sites (i.e. regardless of devil abundance).

Species ecology, like body size, will influence the interactions of heterospecifics. Browsing species, pademelons and wallabies, are more wary and emerge later at night than grazing species. They spend the majority of their time hiding and foraging in dense vegetation to avoid detection from predators as they are generally smaller and less capable of successfully fleeing from a threat. This behaviour was apparent in the results where pademelons had later emergence times from cover and shorter emergence distances from cover than kangaroos. Grazing species, such as kangaroos, are more suited to open landscapes, sheltering in vegetation much later in the morning, and emerge from cover in the earlier in the afternoon with the greatest emergence distances from cover (le Mar and McArthur, 2005). Wallabies are an intermediate-sized species and act as both browsers and grazers, with behaviours like both kangaroos and pademelons. Wallabies emerged later from cover than pademelons, but before kangaroos, and had intermediate emergence distances from cover.

In addition to these ecological niche effects, in the absence of predators, prey may inhabit a greater range of microhabitats and make use of the greater variety of foraging types (Berry et al., 2019). When predators are present, macropods will favour shelter over food (Fisher, 2000). This results in later emergence times from cover and the decrease in emergence distance from cover, to increase the proximity to shelter in the event of predator attack. This behaviour was observed in pademelons, which would have greater perceived levels of threat in their environment due to being highly susceptible to diurnal and nocturnal predators. Larger species, requiring more food, may favour foraging over shelter more often than smaller species (Dawson, 1989). Wallabies and kangaroos are

less vulnerable to quoll, cat or eagle predation as adults and will select for access to high quality feed, further from cover, to ensure their caloric needs are met.

Influence of time of day

The highest vigilance scores and greatest FIDs were observed in the morning and the lowest vigilance scores and shortest FIDs were observed at night. This was a trend seen in all three species of macropod. This is a result of the trade-off behaviour of between nocturnal and diurnal predators in the environment. Macropods must be able to assess the threats of nocturnal and diurnal predators to determine which predators are more important to avoid. This behavioural pattern was held irrespective of devil density, apparent at all three study sites. Diurnal predators may be maintaining the landscape of fear and buffering the impact of devil decline/increase on macropod behaviour (Save the Tasmanian Devil Program, 2018)

White-bellied sea eagles and wedge-tailed eagles, are known to prey on all three species of macropods (Debus, 2019, Olsen, 2014, Fuentes and Olsen, 2015, Debus and Rose, 1999). Birds of prey become active early in the morning and will hunt throughout the day until sunset. First thing in the morning, eagles are hungry and eager to hunt, and being aerial predators, they may be more difficult for macropods to detect and flee from than terrestrial predators, so high levels of vigilance in macropods are needed for safety (Debus, 2019). Mesopredator release of quolls may have also increased the predation pressure of pademelons during the temporal niche of quolls at dusk (Jones and Barmuta, 1998).Emergence distances were also greatest at night, when there was no risk of diurnal predators, either eagle or quoll predation, showing that this is when macropods felt the least threatened in their environment, most susceptible to predation from one predator, devils. As devils usually emerge from cover to hunt, greater emergence distances at night reflected macropod avoidance of devils, whereas high vigilance scores and large FIDs in the early morning (and hiding behaviour throughout the day) illustrated the macropod's wariness of birds of prey (Hamede et al., 2009). Time of day had a greater influence on the behaviour of smaller, more vulnerable individuals, which had greater disparities in behaviour between morning and night observations than in adults.

Influence of vegetation structure

Devil decline was expected to have cascading effects on the ecosystem. Devils, being the top predator, prey on almost all species in their environment and their abundance was expected to have direct influence on antipredator behaviour of prey (Cunningham et al., 2018). However, this influence may have been modified by the changes in vegetation structure (Barrios-O'Neill et al., 2015). The relationship between vegetation density and predation is complicated. With increasing

density of vegetation cover, there is a decrease in predator-prey interactions as prey are more capable of evading detection by predators. However, with increasing population density, either predator or prey species, this interplay between vegetation and predation risk is overridden (Scheinin et al., 2012). With greater predator density, there is an increase in the risk of predation, but with greater density of prey there is a reduction in the individual risk of predation, which relates to the theory behind group size effects (Coulson, 2009, Coulson, 1993). The variation in risk-sensitive behaviour among species in this study is potentially impacted by the density of each prey and devil population at each site. For example, at Maria Island National Park, macropods are so abundant that culling occurs annually to prevent overpopulation (Ingram, 2019). This high density of macropods may have reduced the influence of predator introduction on macropod behaviour.

Animal behaviour, including antipredator behaviours, can also be influenced by the restructuring of vegetation in the environment. Vegetation infringement from forest into open pastures causes an increase in vegetation density at forest edges. This increases the protective cover that forest edges provide for prey and increase the quality of forage (forest edges have greater plant biomass than inner-forest, densely wooded areas) (Scheinin et al., 2012). Foraging in less dense vegetation increases access to greater plant biomass at the danger of greater risk of predation (Fisher, 2000, While and McArthur, 2006, Carter and Goldizen, 2003). Ambiguous forest edges, with obscuring vegetation, can decrease the visibility of the surrounding environment, making it difficult for prey species to detect approaching predators. Devils are pounce-pursuit predators, with a hunting strategy of running along forest edges to encounter herbivores moving between daytime refuge in the forest and night-time grazing in the open (Jones, 2003). Some prey species, for example brushtail possums, depend on visual cues of predators and prefer open vegetation at ground level, that offers good line-of-sight vision of approaching predators when they forage on the ground (Hollings et al., 2015b). It is likely that macropods rely mostly on both visual and auditory cues (While and McArthur, 2006, le Mar and McArthur, 2005, Baynes, 2007).

All three study sites had been historically cleared for use as farming land prior to their establishment as national parks. Narawntapu National Park has had some vegetation regrowth on the forest and woodland edges into the open grasslands, but as it was originally an open marshland that was drained, not much more vegetation regrowth is expected to occur. Maria Island was extensively farmed for many decades and is only starting to show some regrowth in recent years. This is reflected in macropod behaviour, as all species have the shortest emergence distances from cover at Maria Island National Park. Wukalina/Mt William National Park has had abundant and obvious vegetation regrowth and encroachment onto open grasslands since its establishment as a National Park in the 1970s (PWS, 2019). Vegetation regrowth has significantly changed the structure of the

forest edges, with bracken extending well into the open landscape, creating areas for smaller animals to hide during both the day and night. At wukalina/Mt William National Park, kangaroos and wallabies had greater emergence distances than at the other two sites, whereas pademelons did not. Pademelons likely benefitted from the vegetation infringement as it increased the opportunity for them to hide while still taking advantage of the high-quality vegetation in the more open landscape. Wallabies and kangaroos may have become more wary as it may have become more difficult to detect predators emerging from the forest edges to hunt.

Influence of changes in predator density and observer effects

The 'before' and 'after' data sets were collected 10 (Nielsen, 2009) and 18 (Blumstein and Daniel, 2003) years apart. Behavioural changes can occur within a single generation or over a few weeks or months so the timeframe of the 'before' and 'after' data collection periods are sufficient for behavioural changes to have occurred (Bytheway and Banks, 2019, Foster, 2013). Generic anti-predator or risk-sensitive behaviours can be maintained by the presence of other types of predators in the environment, including other mammals or raptors, or even in the absence of predators in the environment (Blumstein and Daniel, 2002, Blumstein, 2006, Blumstein and Daniel, 2005). The 'ghosts of predators past' hypothesis outlines that antipredator behaviours may persist in a population for many generations even in the absence of predators which they were evolved to protect against (Peckarsky and Penton, 1988). As a consequence, the expression of antipredator behaviours may persist with or without predators. My results indicate the maintenance of anti-predator behaviours in the complete absence of devils or long-term suppression of devil populations. Macropods at Narawntapu National Park have maintained high levels of risk-sensitive behaviour for 10 years without the pressure exerted from a top mammalian predator(Hawkins et al., 2006) . Similarly, macropods at wukalina/Mt William National Park have maintained risk-sensitive behaviours even after 22 years of very low population density of devils (McCallum et al., 2007, Lazenby et al., 2018). Devils at this park are deemed to be functionally extinct with respect to ground-foraging behaviour of brushtail possums, which is only usually observed in environments lacking devils in other parts of Tasmania (Hollings et al., 2015b). At Maria Island National Park, macropods exhibited anti-predator behaviours even before devils were introduced (Blumstein and Daniel, 2003, Nielsen, 2009).

Some of the differences in macropod behaviour between time periods we can only attribute to the effect of different observers. Change in the abundance of devils (the 'before-after' time period) and observer are completely and unavoidably confounded in this study, in which I compared a new field data with historic data. The potential for observer bias was reduced in the study design by using

identical field methods. Even if the methods are straightforward and unambiguous to implement and can be repeated exactly as they were originally applied, it is not possible to always control for all factors which may have influenced the results in the original dataset. This restricts the possible comparisons between datasets which can be made. To produce valid results in the comparisons of these past datasets with the 2019 dataset, great emphasis was placed on ensuring comparable types of data were collected and analysed. This is why some components of the 'before' datasets were not included in the analyses. I did not include the vigilance data collected by Ann Nielsen (2009) as she recorded vigilance in field with a stopwatch and an assistant scribing to a paper data sheet. She did not use video recordings or the quantifying program, *JWatcher*, which were used to determine vigilance scores for both Blumstein and Daniel (2003) and 2019 datasets. Nielsen (2009) results had lower vigilance scores than both other datasets, despite Blumstein and Daniel (2003) results obtained in environments of the same devil abundance (Appendix C). Therefore, they were not used in formal comparative analyses.

Nielsen's (2009) dataset did not show a great site influence in vigilance scores for all three species. Narawntapu National Park had slightly higher vigilance scores, however not much greater than wukalina/Mt William National Park which had a much lower abundance of devils. At Maria Island National Park, where no devils were present at all, vigilance scores were still relatively high. This supports the idea that vigilance behaviour can be maintained in environments both with and without top predators (Blumstein, 2006). My dataset reflects similar trends to Nielsen (2009), with the greatest vigilance behaviours seen at Narawntapu National Park for all three species. My results show greater vigilance at Maria Island National Park in 2019, than the macropods observed by Nielson (2009), but as no major changes in macropod behaviour were seen over time periods between Blumstein and Daniel (2003) and 2019, this discrepancy is likely due to observer influence.

Blumstein & Daniel (2003) did not sample all species at all sites which resulted in some deficiencies in 'before' period data for all three species in the vigilance and FID measurements. FID methods for the 2019 fieldwork was replicated from Blumstein & Daniel (2003) methods. However, the results showed large reductions in FID in the 2019 dataset compared to 2001 at all sites, irrespective of devil density. Application of the FID methods in the field seem unambiguous and therefore were assumed simple to replicate, however the results from the 2019 dataset lead me to believe otherwise. One explanation for this may be differences between observers which were out of my control. Such differences could include sex, size/height (e.g. human females may be smaller and less threatening than human males) or appearance of the observer (e.g. different clothing). FID may also be a species specific trait, with some species becoming more easily habituated to human interference in their environment than others (Blumstein et al., 2003).

Human habituation and interaction can cause for changes in risk-sensitive behaviours in wild populations of animals (Sih, 2013, Price, 2008). Overtime, increased non-lethal contact with humans will decrease the wariness of macropods towards people (King et al., 2005). Tourists are common at all three study sites and therefore may have influenced the behaviour of the animals surveyed during the 2019 dataset. Macropods present at Maria Island National Park have become so habituated to human presence that pademelons were seen foraging in the campgrounds at most hours of the day. Pademelons were also present in large groups at dusk and at night and Narawntapu National Park campgrounds. I minimised the effect of habituation from increased tourism by surveying macropods that live well outside (1-10 km away) the areas in all three sites that have high levels of human activity. Although I cannot exclude the possible influence of habitation to people on the study results, it is unlikely to have been significant. If habituation to humans influenced the results, I would expect reduced FIDs, reduced vigilance and earlier emergence at all sites, and particularly on Maria Island National Park which has the highest visitor numbers. This was not the case.

Non-predatory environmental influences and species and individual traits are shown to be the most influential factors of risk-sensitive behaviour in Tasmanian macropods. Vegetation regrowth acts as a mechanism maintaining a landscape of fear in environments with minimal top predator pressure. Although, it is important to consider that ecosystem changes which have occurred at these study sites have been related to the loss of human-induced environmental change, such as the cessation of clearing for farming land.

At Maria Island National Park, devil densities changed from absent to carrying capacity, whereas at Narawntapu National Park densities declined 90% from the original population (Thalmann et al., 2015, Epstein et al., 2016). These adjustments to devil predator pressure experienced by these macropods at these sites are able to cover the full range of densities which would naturally be expected anywhere. The results are able to measure large changes in top predator density to be applied to other research.

Top predator loss or gain did not have strong influences on the antipredator behaviours of macropods that I measured: vigilance behaviour when they were recorded foraging in the open, and the time in the afternoon and night that macropods emerged from the shelter of the forest. Putting together these results with different measures of risk-sensitive behaviours recorded by Cunningham et al. (2019a) and (Cunningham et al., 2019b), there are some responses of macropods and other prey species of devils to devil decline and introduction. Cunningham found stronger responses of prey species to an increase in devil density than occurred with declining devil density. Brushtail

possums are smaller than any of the macropods researched in this study but are a major prey item for devils (Andersen et al., 2017, Jones and Barmuta, 1998). Possums were highly responsive to changes in devil density, increasing their foraging particularly away from the refuge of trees which offer escape when devils declined on mainland Tasmania (Hollings et al., 2015b). As devil density increased on Maria, possums reduced their foraging (higher GUDs) (Cunningham et al., 2019a). As an arboreal folivore, proximity to trees which they can climb to escape from devils, are an important component of their antipredator behavioural strategy. Cunningham et al. (2019b) found that pademelons altered their spatio-temporal use of the landscape, being slightly more active (not statistically significant) at sunset and sunrise on mainland Tasmania as devil density declined. Greater activity at sunrise is reflected in my study in the greater number of videos that were collected of pademelons at Narawntapu in 2019, compared to none in 2001 (Blumstein and Daniel, 2003). increasing their activity at sunset when devil density was high, although their temporal pattern of foraging behaviour still overlapped with the temporal niche of devils, possibly because predators follow the activity of their prey (Cunningham et al., 2019b). Wallabies altered their temporal niche to reduce the chance of encounter with devils in response to devil introduction on Maria Island, with a shift to after sunrise (Cunningham et al., 2019a, Cunningham et al., 2019b). All macropods in my study were more vigilant across all sites in the morning, after sunrise, probably in response to diurnal predators at all sites. Where devils are at higher density, they would push the activity of macropods into the morning period, increasing the overall risk of predation. Larger species such as also responded to increasing devil density, peaking in activity before sunset to significantly reduce their temporal niche overlap with devils (Cunningham et al., 2019b). Wombats are larger and tougher to kill for devils than wallabies but devils do prey on juveniles (Jones and Barmuta, 1998).

6. **Conclusion**

There was no strong predator influence on the antipredator behaviours of macropods in response to the decline or introduction of Tasmanian devils in the environment. Through the comparison of historic and current data sets, results did not show any changes in macropod behaviours in response to alterations in predation threat. However, changes in the structural complexity of the environment, such as vegetation infringement, and attributes of individual macropods, such as ecological niche, body size and age, had strong influences on the expression of risk-sensitive behaviour in macropods. This indicates that the relationship between predator and prey is much more complex than previously assumed, and is influenced by many interacting factors, such as the diel cycle and the presence of other predators in the environment.

I conclude that modifications in prey behaviour may not always reflect changes in predator pressure, therefore prey risk-sensitive behaviours should not be used to determine the influence of predator loss or gain in an ecosystem. Future research would be beneficial in determining the factors influencing prey responses to predator abundance. In the Tasmanian context, this could involve conducting research on macropods, devils and the influence of vegetation structure. Captive studies involving captive-bred devils and macropods may also be useful in understanding the flexibility of macropod behaviour in response to environmental pressures (Griffin, 2003).

The outcomes of this study change the way in which scientists should think about the impacts of the conservation and regeneration or reintroduction of top predators. Top predators have great influences on the ecosystem, but their interaction with prey species is multifactorial (Duffy et al., 2007). Vegetation structure greatly influences the responses of prey individuals to predator pressures by shaping the landscape of fear and the perceived level of threat in the environment (Scheinin et al., 2012). The conservation and regeneration of top predators should consist of not only maintaining predator abundance, but also maintaining the physical structure of the ecosystem. This research also proves that introduction of predators into historically absent areas is possible without causing detrimental effects on the existing ecosystem. In conclusion, detailed and mechanistic analyses of the factors which influence the behaviours and the interspecific interactions of native species are needed to understand predator-prey relationships in their natural landscapes.

7. **References**

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8. **Appendix**

Appendix A – Transect IDs and lengths

Transect	wukalina/Mt William	Maria Island	Narawntapu
Pilot	405 metres	270 metres	360 metres
1	315 metres	-	315 metres
1A	-	225 metres	-
1B	-	225 metres	-
2	270 metres	-	-
2A	-	-	135 metres
2B	-	-	180 metres
3	225 metres	-	-
3A	-	-	180 metres
3B	-	-	90 metres
TOTAL (excl. sample)	**810 metres**	**450 metres**	**900 metres**

Table A: Transect identification and lengths at the three Tasmanian study sites: wukalina/Mt William National Park, Maria Island National Park and Narawntapu National Park.
Note: pilot transects were only set up during the first fieldtrip to each site. They were set up in the same location of transect 1 at each site (transect 1A at Maria). Only the singular pilot transect was set up during the first fieldtrip to each site and to compensate for this, the pilot transects were longer than the subsequent transects in the following fieldtrips.
A and B transects were walked as singular transects, only split in two due to vegetation infringement.

Appendix B – Google Maps plates of transects

Plate B1: Google Map plate of transects 1A (blue) and 1B (red) at Maria Island National Park, Tasmania, Australia. The plate shows the grid formation of transects which made it quick and easy to determine the location of a subject on the transect and determine its distance from the forest edge. Arrows represent the 5th pickets where the observer commences walking along the transect.

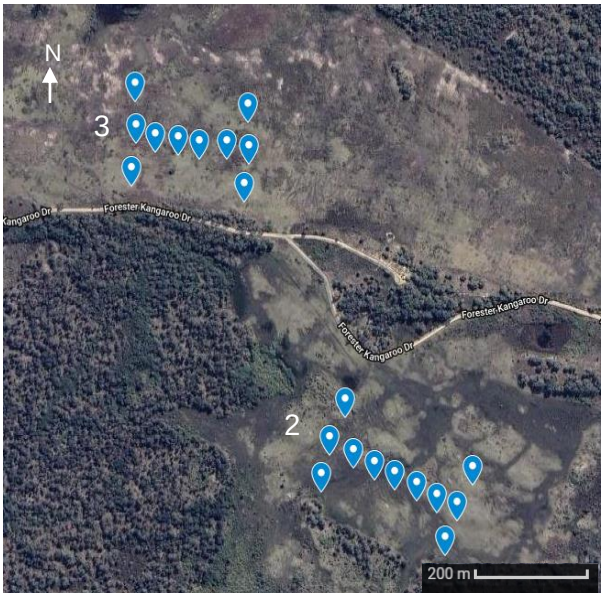

Plate B2: Google Map plate of transect placement at wukalina/Mt William National Park, Tasmania Australia. Only the outline and the walking line of transects are shown (not all the pickets are marked).

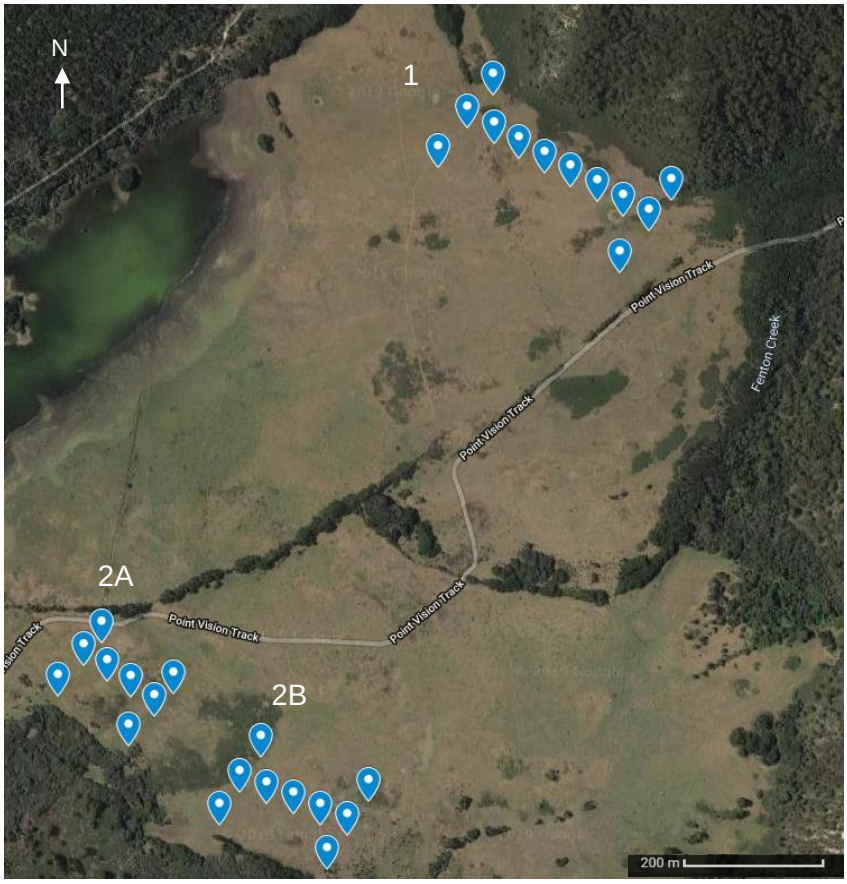

Plate B3a:
Google Map plate showing transect 1 and 2 placements at Narawntapu National Park, Tasmania Australia. The plate shows the split of transect 2 into sections A and B. This was due to vegetation infringement at the centre of the transect location, potentially concealing smaller macropods from observer view. Only the outline and the walking line of transects are shown (not all the pickets are marked).

Plate B3b:
Google Map plate showing transect 3 placement at Narawntapu National Park, Tasmania Australia. The plate shows the split of transect 3 into sections A and B. This was due to vegetation infringement at the centre of the transect location, potentially concealing smaller macropods from observer view. Only the outline and the walking line of transects are shown (not all the pickets are marked).

Appendix C – Vigilance score comparisons between 2001, 2009 and 2019

I modelled the proportional response variable within a generalised linear model framework by converting the data to a binomial family structure (Crawley, 2015). Fifty samples (n=50) from the data set for each video were used to determine the number of successes or failures (with regard to vigilant activity), where the number of successes = x and the number of failures = (n-x). Generalised linear mixed models (GLMMs) were then used to compare the influence of observer on the response variable, the vigilance behaviour of individuals. The random factor was the replication represented by individual videos. Analyses were completed only for common site-species combinations. These were pademelons at Narawntapu (Figure C1) and wallabies and kangaroos at both Maria and wukalina (Figures C2-C5)

Initial exploratory analyses indicated that Nielsen's (2009) scores for vigilance were generally higher than both the 2001 (Blumstein & Daniel 2003) and the 2019 (Emilie Roure) datasets, most likely due to methodological differences. As a result, her data was not used for vigilance analyses.

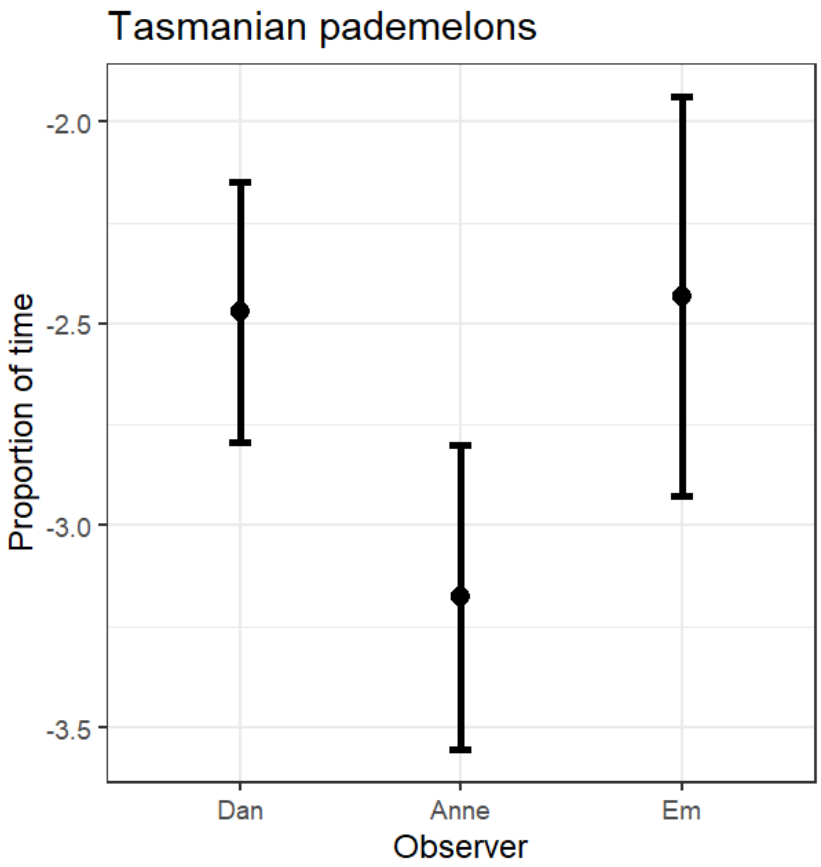

Figure C1: Plot of the observer effect of the proportion of time spent vigilant of Tasmanian pademelons at Narawntapu National Park in 2001 (Daniel Blumstein), 2009 (Anne Nielsen) and 2019 (Emilie Roure).

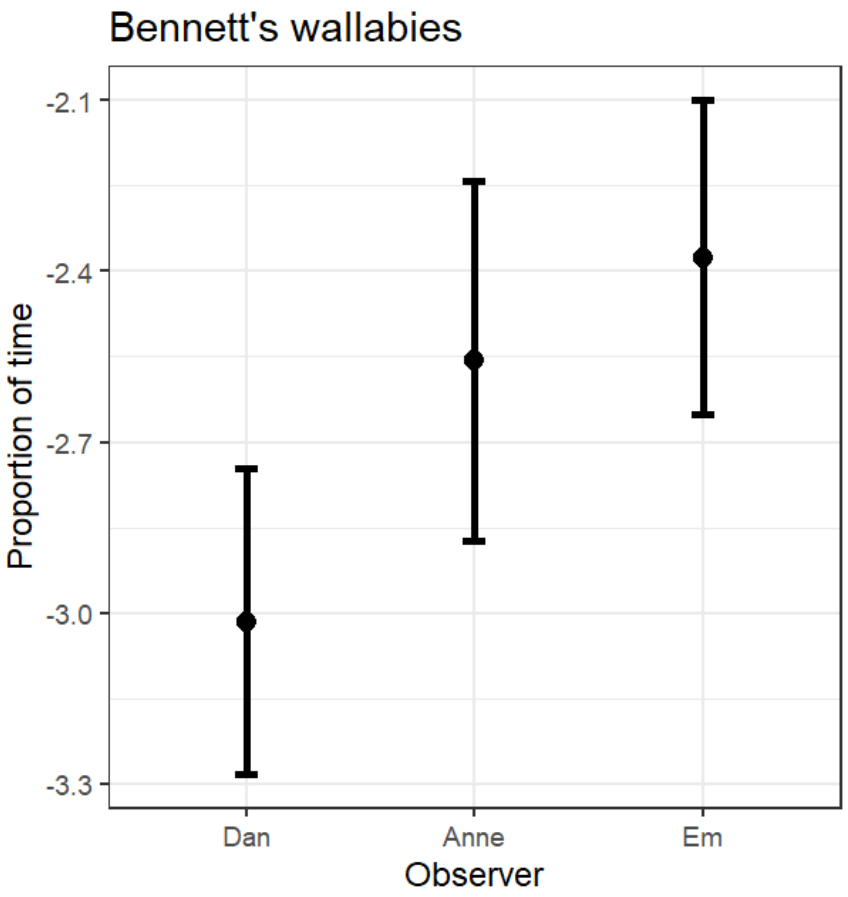

Figure C2:
Plot of the observer effect of the proportion of time spent vigilant of Bennett's wallabies at wukalina/Mt William National Park in 2001 (Daniel Blumstein), 2009 (Anne Nielsen) and 2019 (Emilie Roure).

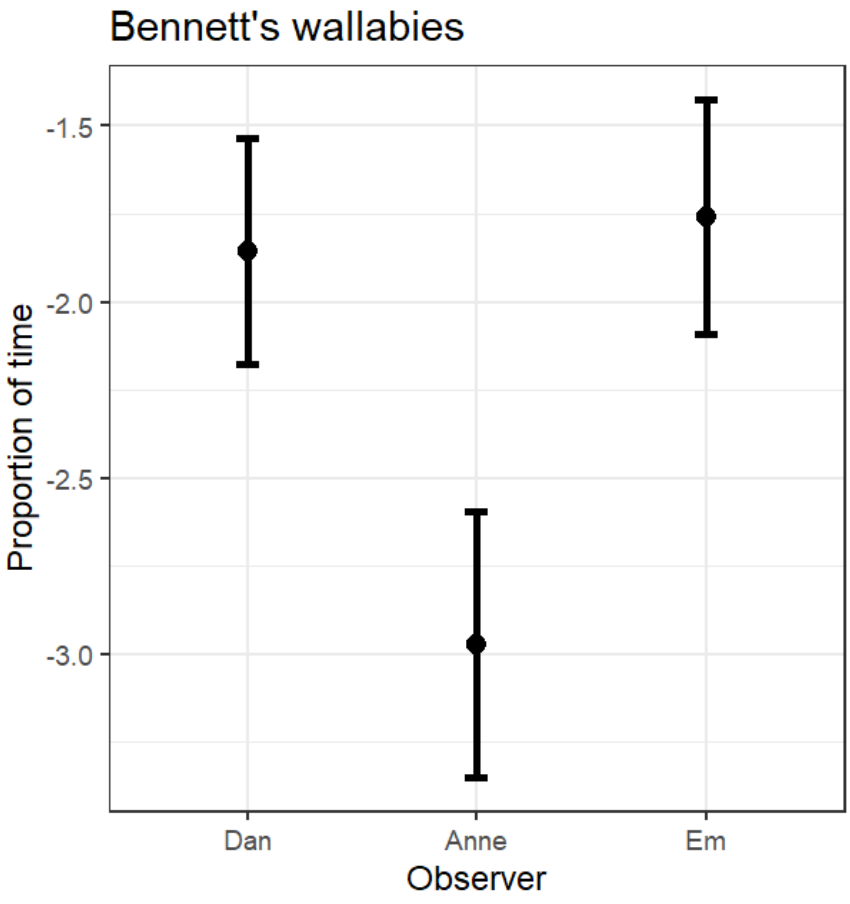

Figure C3:
Plot of the observer effect of the proportion of time spent vigilant of Bennett's wallabies at Maria Island National Park in 2001 (Daniel Blumstein), 2009 (Anne Nielsen) and 2019 (Emilie Roure).

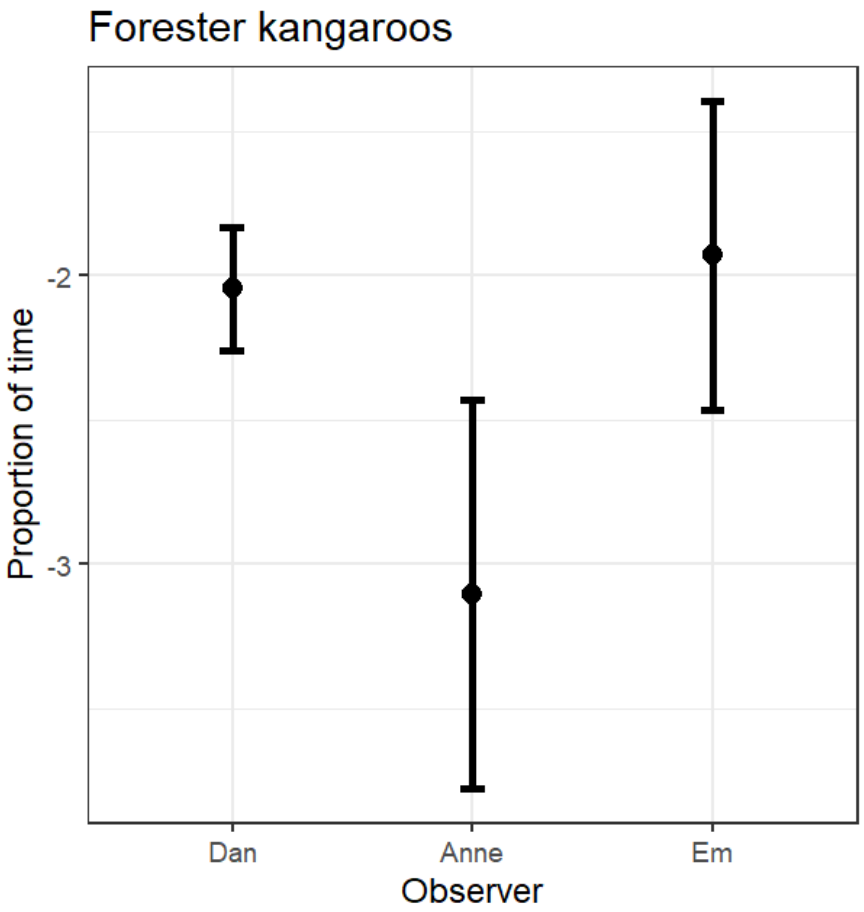

Figure C4:
Plot of the observer effect of the proportion of time spent vigilant of Forester kangaroos at wukalina/Mt William National Park in 2001 (Daniel Blumstein), 2009 (Anne Nielsen) and 2019 (Emilie Roure).

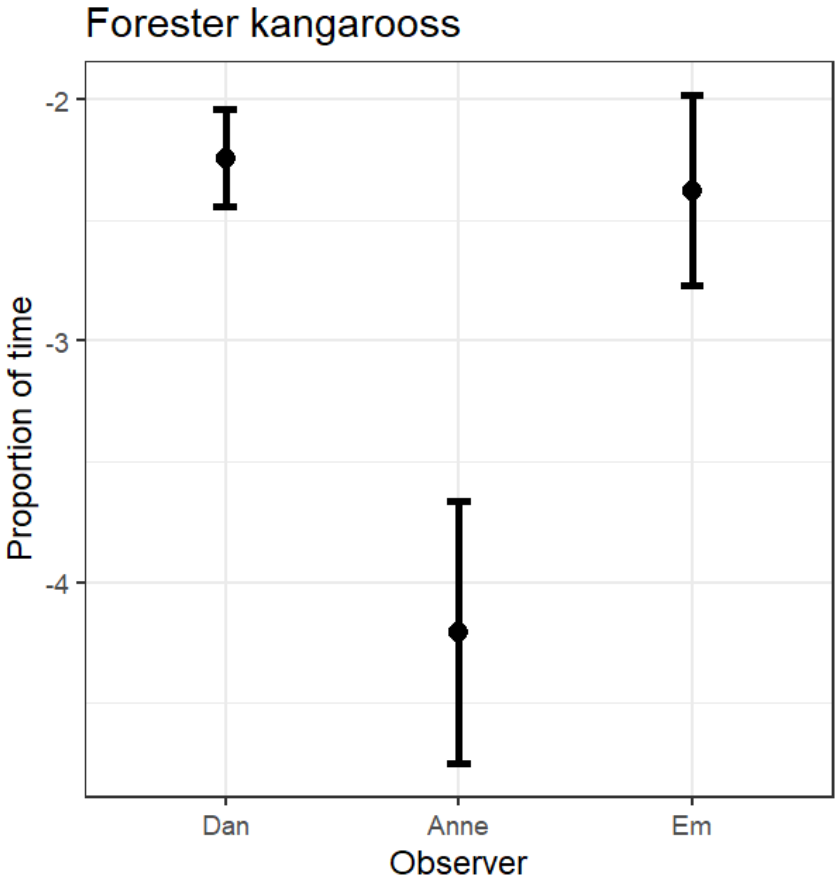

Figure C5:
Plot of the observer effect of the proportion of time spent vigilant of Forester kangaroos at Maria Island National Park in 2001 (Daniel Blumstein), 2009 (Anne Nielsen) and 2019 (Emilie Roure).

Appendix D – Emergence times from cover in 2009 and 2019

2009	Timeslot→	BD	D	N	M
Site	Species				
M	P	0	96	88	72
	B	0	62	55	58
	F	80	49	57	41
N	P	6	371	584	594
	B	39	112	77	87
	F	34	6	1	3
W	P	5	79	81	60
	B	181	354	332	396
	F	54	35	35	18
Total (all sites)	P	11	546	753	726
	B	220	528	464	541
	F	168	90	93	62

Table D1:
Number of species present on transects at each National Park during the four different for the 2009 (Anne Nielsen) dataset.

2019	Timeslot→	BD	D	N	M
Site	Species				
M	P	6	4	54	74
	B	6	6	32	50
	F	145	73	84	156
N	P	1	29	429	368
	B	39	134	113	113
	F	201	55	33	33
W	P	1	5	131	98
	B	75	173	166	162
	F	9	9	2	1
Total (all sites)	P	8	38	614	540
	B	120	313	311	325
	F	355	137	118	191

Table D2:
Number of species present on transects at each National Park during the four different timeslots for the 2019 (Emilie Roure) dataset.

KEY

Species → P = Tasmanian pademelon,
B = Bennett's wallaby,
F = Forester kangaroo

Site → M = Maria Island,
N = Narawntapu,
W = wukalina/Mt William

Timeslot → BD = before-dusk,
D = dusk, N = night, M = midnight

9. **Literature Review**

Is facilitating rapid evolution a feasible and effective way of reducing the impacts of invasive predators on native prey?

9.1 Abstract

Invasive species heavily influence the demographics and behaviours of native prey species. Native prey which are naïve to novel, invasive predators, experience high selection and increased death rates if they are unable to respond to their threats appropriately. Conducting a systematic literature search on the relationship between invasive predators and native prey revealed the underrepresentation of literature on rapid evolution. Rapid evolution is one way in which animals adapt to changes in their environment. It relies on heritable changes being selected for and passed on through a population. In order to test whether facilitated rapid evolution is effective in wild prey populations, more information is needed about how it is facilitated and its timescale of action. This review is able to conclude there is great variation in the timescale over which rapid evolution occurs. The literature has shown that *in situ* predator exposure is the most effective way of facilitating rapid evolution for the rehabilitation of captive prey species. More research is needed in order to determine if this is also the most effective method for promoting rapid evolution in wild prey species.

9.2 Introduction

The introduction of predatory species which lack co-evolutionary history with native species is a major threat to biodiversity. Invasive species are among the main drivers of species loss in native environments (Farnsley et al., 2018, Salo et al., 2007, Spencer et al., 2016). The prominent invasive species around the world today originate from Europe during the European expansion. These are generally placental mammals, such as the dominant mammalian fauna in Eurasia, Africa and North and South America (Cox and Lima, 2006, Carthey and Blumstein, 2018). In islands that have been isolated from these continents for thousands of years, such as New Zealand, Australia and Madagascar, native animals lack co-evolutionary history with these invasive species (Remeš et al., 2012, Monks et al., 2019). Native species suffer pressures through competition for resources or

through predation as they are unable to recognise these novel predators as threatening (Chivers et al., 2001, Sih et al., 2010).

Alien predator species are often morphologically and behaviourally distinct from native species (Blake et al., 2015). The extent to which native prey will recognise alien predators depends on the predator's resemblance to historical predator archetypes (Cox and Lima, 2006). Predator archetypes are made up of species with similarities in traits. One example is the similarities in morphology and behaviour among predatory species in the cat family Felidae (Cox and Lima, 2006). The outcomes on native fauna from introductions of feral cats (*Felis catus*) and red foxes (*Vulpes vulpes)* in Australia 150 years ago, contrast to the associated consequences of dingo (*Canis dingo*) introduction 3500 years ago. Native fauna had difficulty in detecting and responding to the chemosensory cues of these placental predators which secrete different chemical compounds to marsupial mammals. They failed to recognise foxes and cats as a predator (Carthey and Banks, 2014, Berry et al., 2019, Short et al., 2002, Carthey et al., 2017, Carthey, 2013, Mella et al., 2014). Dingoes, however, did not only have the same canid-like predator archetype as the historic predator, the thylacine (*Thylacinus cynocephalus*) but, unlike the canid red fox, are of a similar size to the thylacine (Savolainen et al., 2004, Fillios et al., 2012). Native prey species, already having established antipredator behaviours to respond to thylacine predation, would have been able to recognise and respond to this medium-sized canid species. True alien predators will have the greatest effects on prey species as their appearances and behaviours are unfamiliar. Feral cat felid morphology and surplus killing behaviour in foxes are examples of this in the Australian context (Sih et al., 2010, Short et al., 2002).

Prey may alter behaviour, morphology and physiology in response to threats in their environment (Blumstein and Daniel, 2002, Blackburn, 2004). This may be in response to loss of exposure or extended isolation from predators. The naïve prey hypothesis proposes that evolutionary inexperience is the cause of inappropriate antipredator behaviour of native prey species towards invasive predators (Saul and Jeschke, 2015, Cox and Lima, 2006, Sih et al., 2010). Prey which fail to detect a potential predator and lack the appropriate antipredator behavioural response, exhibit prey naiveté (Atkins et al., 2016, Banks et al., 2018). Naiveté has been documented in a wide range of animals, from mosquitofish (*Gambusia geiseri*) to ladybirds (*Adalia bipunctata*) and can occur in a number of scenarios (Blake et al., 2015, Roy et al., 2012). Extended isolation from a predator species can result in prey species becoming unfamiliar to the predator archetype and result in a reduction in antipredator behaviour types.

Changes in response may become costly, morphologically or energetically, to maintain and are lost when they are no longer necessary for survival (Blumstein, 2006). Blumstein (2002) shows that in

tammar wallabies (*Macropus eugenii*), isolation from predators causes rapid loss of experience-dependant behaviours such as flight initiation distance. A population of quolls (*Dasyurus hallucatus*) isolated on an island for 13 generations showed a complete loss of recognition and response towards a historic mainland predator (Jolly et al., 2018b). Exposure to multiple predator archetypes can shield prey species against intense predation thresholds from an invasive predator due to their greater variety of pre-existing antipredator behaviours (Ehlman et al., 2019). The multi-predator hypothesis predicts that traits are linked with one another, and therefore, the loss of a single predator is likely to have limited influence on overall antipredator behaviour (Blumstein, 2006, Carthey and Blumstein, 2018). In some instances though, the loss of one predator type is able to cause the loss of one corresponding antipredator behaviour (Blumstein and Daniel, 2005). Kangaroos (*Macropus spp.*) living on Kangaroo Island in the absence of dingoes often forage on their own. Mainland populations of this species continue to forage in groups to protect themselves and their young from potential dingo attacks (Blumstein et al., 2002). Group foraging behaviour was lost relatively rapidly on Kangaroo Island, as it was no longer needed for protection from dingos, and individual foraging behaviour increases individual foraging rate.

There is a paucity of literature in the area of rapid evolution in response to invasive predators despite the strong selection pressure that alien predators inflict on prey species. To better understand the scientific knowledge on rapid evolution, I will analyse the current literature against two frameworks: (1) naiveté and (2) mechanisms of response to novel predators, to highlight why there is insufficient literature on this process and the potential areas for future research. This will then establish how future studies can research the process of rapid evolution in wild populations to improve its application in re-establishing declining wildlife populations.

9.3 Methods

For this review, systematic searches were done through Scopus, selecting and excluding specific search terms to refine results to produce 636 papers (Figure 1). These papers were then filtered manually and those which were found to be applicable to this review were selected. This is not a systematic review however, as not all applicable papers were included, and some papers found through additional, more specific search methods were also used in this review. Additional research was needed to ensure there was enough relevant literature on the topic of rapid evolution. Papers had to be published recently, between 2000 and 2019, to ensure that the literature cited is current and relevant. Although rapid evolution is not a new topic of research, recent studies have shed light to novel discoveries of its mechanism which may not have been reviewed in previous studies.

Search terms	**Exclusions (words)**	**Exclusions (subject area)**
Native W/2 prey	Agri*	ENGI
Indigenous W/2 prey	Econom*	SOCI
Endemic W/2 prey	Infect*	MATH
Natural W/2 prey	Disease*	BUSI
Local W/2 prey	Child*	ARTS
Novel W/3 predator	Virus*	ECON
Alien W/3 predator	Politic*	DECI
Exotic W/3 predator	Yield*	PHYS
Invasive W/3 predator	Isotop*	MATE
Introduced W/3 predator	Food*	ENER
New W/3 predator	Sleep*	VETE
Novel W/3 threat	Conscious*	CHEM
Introduced W/3 threat	“Pest control”	CENG
Detect*	Engine*	DENT
Identif*	“climate change”	IMM
Respon*	Livestock*	PHAR
Recogni*	Molecule*	NURS
React*		HEAL
Behav*		UNDEFINED

Figure 1*: Systematic search through Scopus*.

This selection of search terms was used to refine the literature output in search engines. This reduced the amount of time needed to sort through each paper to determine its relevancy.

9.4 Results and Discussion

Section One: How do naïve species become competent?

Naïve prey populations experience strong selection pressures. Individuals that are able to overcome these selection pressures become competent in responding to novel threats and survive to coexist with novel predators. Figure 2 summarises the four levels of prey naiveté in prey species in response to these predators (Banks and Dickman, 2007). Prey must overcome these four levels of naiveté to develop effective predator awareness and antipredator behaviours (Bytheway and Banks, 2019). Different species and different individuals within a species population may take longer than others to develop this experience.

Selection pressures can increase predator awareness. This can occur by three mechanisms: plasticity, learning and evolutionary modifications (Figure 3)(Carthey and Blumstein, 2018). These mechanisms have different timescales of response, influencing their frequency in a population. Plasticity occurs at the individual level and can take less than one generation to become prevalent in a population (Brookes and Rochette, 2007, Renn and Schumer, 2013). Learning can also occur at the individual level but usually becomes apparent in a population after its second generation of prevalence (Bytheway and Banks, 2019). This process occurs when a younger individual is taught a skill or behaviour by another older, more experienced conspecific. Rapid evolution of a population occurs through heritable changes in individuals over time. These heritable changes take multiple generations to become widespread in a population (Sih et al., 2011). Natural selection is effective in selecting the best suited individuals for survival, especially in relation to individuals that are best suited to survival against predators in the environment (Carthey and Blumstein, 2018).

Plasticity involves the neurological rewiring and strengthening of pre-existing antipredator behaviours in response to a novel threat. It is the quickest mechanism of change as it involves a pre-existing template in the genotype which allows for an immediate response to changes in the environment (Gross et al., 2010). Behavioural plasticity is the ability of a genome to generate varying phenotypes depending on changes in the environment (Foster, 2013, Renn and Schumer, 2013). These phenotypes are activated in response to environmental influences to improve the individual's chance at survival. Activational plasticity involves behaviours produced by a specific change in the environment but only last for short periods of time until this change is no longer present (Westrick et al., 2019, Foster, 2013). This mechanism is especially effective when novel predators share behaviours with historical predators (Hollander and Bourdeau, 2016).

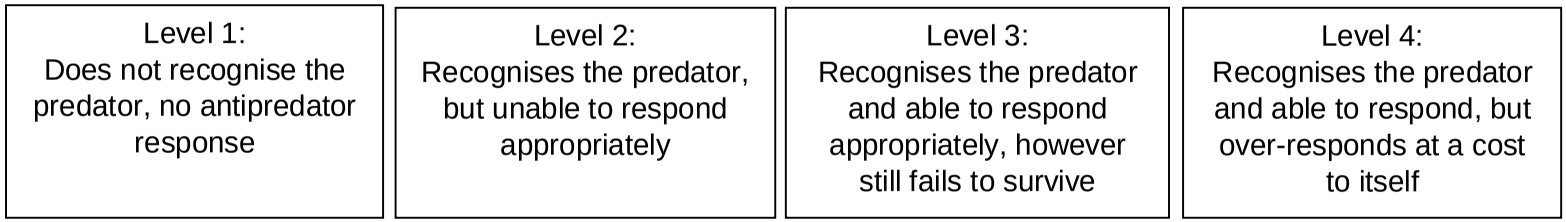

Figure 2: The levels of prey naiveté to invasive predators. (Bytheway and Banks, 2019)

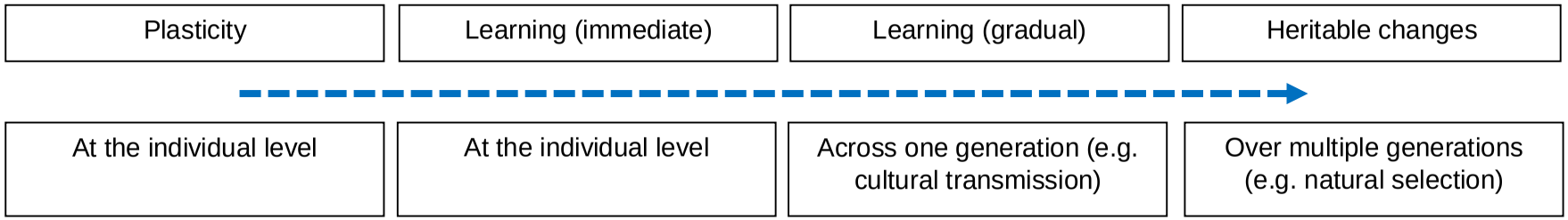

Figure 3: Temporal scale of types of mechanisms of response. (Carthey and Blumstein, 2018)
Arrow in blue indicates order of increasing length of time needed for changes to occur by these mechanisms. It shows that plasticity is the fastest mechanism of change and heritable changes take the longest

Bilbies (*Macrotis lagotis*), which have had evolutionary-scale coexistence with dingos, but not dogs or cats, showed predator avoidance behaviour when exposed to dog odour and no change in behaviour when cat odour was presented. Bilbies were naïve to cat cues but recognised dog cues although they had never had previous contact with dogs. As dogs have the same predator archetype as dingos, the bilbies were able to recognise them as a threat (Steindler et al., 2018). Plasticity is often helpful in acting as a safety buffer, increasing an individual's chance at survival until it learns how to respond to a novel threat (Foster, 2013). Japanese tadpoles (*Rhacophorus arboreus*) with previous exposure to a native predator had a greater survival rate when exposed to a novel invasive predator (Ramamonjisoa et al., 2019). Although the novel predator had a different archetype to historical predators, the tadpoles had an element of plasticity in their antipredator behaviour giving the tadpoles a chance to adapt to the new predator behaviours. Plasticity, being the fastest mechanism of change, will rapidly help prey species overcome naiveté to novel predators and improves the efficacy of rapid evolution in wild populations.

Learning takes longer to establish than plasticity as it involves a 'trial and error' situation, where an animal learns through its experiences (Bytheway and Banks, 2019). Individuals which respond appropriately to predators will survive and remember to use the behaviour when they encounter the predator again. This knowledge can be passed on to other individuals, either to their offspring or to others in the population through cultural transmission (Barbosa and Castellanos, 2005). Those that do not learn, become prey and do not reproduce; consequently, their fitness, intergenerational survival, reproduction and contribution to the gene pool, is reduced to zero. There are two types of learning: direct immediate learning or gradual learning through cultural transmission (Figure 3)(Sih et al., 2011). Many animal mothers teach their young how to identify and react to potential predators. This is apparent in North American moose (*Alces alces)* where orphaned yearlings, which lack guidance from a mother, have more variation in antipredator behaviour than yearlings with mothers (White et al., 2001). Cultural transmission also occurs in populations of adult individuals. A selected group of tammar wallabies were separated and trained to fear a taxidermic fox. In later trials, all wallabies in the population, even those not exposed to the fox, developed antipredator behaviours towards the taxidermic fox (Griffin, 2003). As learning is multi-faceted, resulting in individual and multigenerational change, it is likely to be the most prevalent mechanism in wild populations.

Evolutionary modifications, the third type of predator awareness, arises from natural selection. Pressures in the environment will select for specific traits in individuals that increase fitness and will determine which individuals are best suited to the changing environment (Foster, 2013). Selection operates on individuals, but if the selection has multigenerational effects, there will be an increase in

the prevalence of the adaptive behaviour in the population. Multigenerational effects may occur through cultural transmission or heritable changes. Heritable changes can occur through genetic and non-genetic (epigenetic gene expression) developmental means. Epigenetic change involves genes being switched on or off in response to changes in the environment. Cane toads (*Rhinella marina)* at the edge of their territories have developed physiological and morphological changes (e.g. longer legs) and are known to travel farther and in straighter paths (Shine et al., 2011). Cane toads in these areas would need to be fit for travelling long distances in short amounts of time. As it takes multiple generations of selection before heritable modifications are prevalent in a population, it is a much slower mechanism of action for facilitating rapid evolution.

Section Two: Types of predator cues and prey responses

Prey species must be able to first detect and then correctly recognise cues in order to respond to them appropriately. This is especially important for predatory cues which are time-sensitive, as an unresponsive animal could face a mortal consequence (Sih, 2013). There are a variety of cues which prey species use to detect predators. The majority of these include olfactory (chemosensory), visual and acoustic cues (MacLean and Bonter, 2013, Blumstein, 2002). Depending on the environmental conditions, prey species may choose which cues they will utilise and interact with. Some prey species will ignore chemosensory cues from predators in open areas, as visual cues are more dependable. Other species do not respond to chemosensory cues at all (Parsons et al., 2007, Griffin et al., 2001, Chivers et al., 2001).

Chemosensory cues contain extensive information about an animal, such as its age, sex and potential to threaten other species in the ecosystem through predation (Parsons et al., 2018, Steindler et al., 2018, Nelson et al., 2013). Predator odours can have direct influences on prey behaviour, including the suppression of feeding and grooming, and behavioural displacement of prey to other odour-free microhabitats. The source of the odour, whether from faeces, sweat glands, fur or feathers, also has an influence on the type of prey response (Mella et al., 2016). Extended exposure to predator odour can have damaging effects on breeding success. Female animals are at greater risk of predation when pregnant or with young, and therefore some females avoid mating during periods of prolonged predator presence (Apfelbach et al., 2005). Exposure to predators can also influence the heritability of certain behavioural components. In three-spined stickleback fish (*Gasterosteus aculeatus*), sociability (the preference for protection from conspecifics over protection from shelter) is only heritable in predator-exposed populations (Dingemanse et al., 2009). Visual cues and acoustic cues can indicate the presence of more imminent threats. Animals which rely on visual cues for predator detection must quickly distinguish between predator archetypes and non-

threatening archetypes. Burrowing bettongs (*Bettongia lesueur*) showed an increase in scanning behaviour at feeding stations when exposed to dingo/dog models (Atkins et al., 2016). Acoustic cues (e.g. predator vocalisations) also compel prey animals to make quick informed decisions on threats in their environments. Acoustic cues are known to increase general flightiness in some bird species such as in crimson rosellas (*Platycercus elegans*)(Adams et al., 2006).

Prey species respond to predator cues in a diverse range of ways which can be categorised into three main groups: behavioural, morphological and life history changes (Carthey and Banks, 2016, Whitlow, 2003). Behavioural changes in response to potentially threatening cues can include short- and long-term modifications within an individual (Whitlow, 2003). Short term changes are rapid responses to imminent threats. Moose populations show rapid changes in antipredator behaviour, including changes in foraging habitats, after the reintroduction of wolves (*Canis lupus*) (Berger et al., 2001). This has also been illustrated in other species such as lizards and kangaroos (*Macropus fuliginosus)*(Webster et al., 2018). When kangaroos encounter scent from predator faeces, they adjust their space use and foraging efficacy, moving to more heavily vegetated and sheltered areas of lower forage quality (Mella et al., 2014). In addition to foraging responses, direct behavioural responses to predation threat can cause an increase in bouts of time spent protecting young(Massaro et al., 2008). Black robins (*Petroica traversi*) threatened by invasive, nest-destroying starlings (*Sturnus vulgaris*), alter their nesting behaviour and re-nest closer to the ground to reduce the risk of damage to their eggs and nest (Lawrence et al., 2017). European shags (*Phalacrocorax aristoteli*) also shifted their nest sites after invasive American mink (*Neovison vison*) caused a large decline in the population through predation on shag eggs and young (Barros et al., 2016). These quick changes in behaviour, although direct responses to an imminent threat, may affect the long-term success of a species.

Long-term behavioural changes can occur through the maintenance of short-term antipredator behaviours over long temporal scales. Western sandpipers (*Calidris mauri*) learned to change their stopover duration on specific islands during migration, and spent more time resting on islands with better visibility to reduce the risk of predation by peregrine falcons (*Falco peregrinus*) (Ydenberg et al., 2004). Similarly, burrowing bettongs have improved their antipredator behaviours by having greater flight initiation distances after extended exposure to feral cats (West et al., 2018). Changes in mating behaviour in response to predation have also been extensively studied. Cultural transmission and the inheritance of certain traits has influenced the behavioural adaptations of guppies (*Poecilia reticulata*) to predator cues (Swaney et al., 2015). Female guppies in high risk, predator-exposed environments have greater preference to mate with dull coloured males rather than brightly

coloured males to produce visually discreet sons which are more difficult for predators to prey on (Westrick et al., 2019).

Long-term exposure to stressful environments, such as predator-ridden environments, will cause the release of glucocorticoid hormones, such as corticosterone, from the hypothalamus (Narayan et al., 2013). These high blood levels of glucocorticoid hormone can promote the expression of certain antipredator behaviours, such as hiding. Corticosterone has the potential to influence an animal's response to similar threats in the future, causing long-term effects on animal behaviour and health (Trompeter and Langkilde, 2011). In domestic chickens (*Gallus gallus domesticus*), early-pubertal exposure to stress has negative effects of the development of the hypothalamic-pituitary-adrenal axis which causes an increased level of fearfulness, and potentially a threatens overall health (Ericsson et al., 2016).

Morphological changes often occur in highly selective environments (Whitlow, 2009). An excellent illustration is found in a species of marine gastropod, periwinkles (*Littorina obusata*). When exposed to predatory cues from green crabs, periwinkles produced 91% greater shell mass than unexposed periwinkles which helps protect them from predation by crabs (Brookes and Rochette, 2007). Morphological changes may be influenced by epigenetic changes in the genome. Pacific tree frog tadpoles (*Pseudacris regilla*), found in streams with invasive crayfish (*Procambarus clarkia*) had shallower tail muscles and fins than tadpoles found in crayfish-free streams. Growing a deep, wide tail is helpful for swimming in strong currents but invests more time and resources which are needed for a fast growth rate which is necessary in a predator-ridden environment (Pease and Wayne, 2014). Another study on tadpoles (*Rana dalmatina*) confronted with predators that had consumed conspecifics had an increase in body size and wider tails for fast, powerful swimming in a high risk environment (Gazzola et al., 2018).

Life-history changes can significantly alter the reproductive capacities of an animal population. This includes age at first breeding and consequently population growth rate and persistence (Apfelbach et al., 2005). Life-history changes are often caused by heritable or epigenetic changes in the population. Female mice (*Mus musculus*) exposed to cat odour have been shown to produce smaller litters of young with altered sex ratios (Apfelbach et al., 2005). Damselfish (*Stegastes partitus*) also show a change in life-history traits after exposure to predators where individuals living in reefs with invasive lionfish (*Pterois spp.*) had reduced adult body size and fecundity. The true reason for this lowered fecundity is uncertain, but is likely to correlate with reduced female body size and the restriction of female damselfish visits to spawning sites, thereby reducing the abundance of offspring (Davis, 2018).

From the literature reviewed, there are a range of unique prey responses to predatory threats. Taxa which appear to be quite similar may in fact have vastly different reactions to a new threat. More information on species-specific responses of these reactions are needed to better understand any existing trends in predator response behaviour in order to anticipate how other less studied species may respond in the future.

Section Three: Evolutionary modifications and rapid evolution

Despite the abundant literature on rapid evolution in ecological time scales, there are relatively few case studies documenting rapid evolution in prey species in response to predation pressure. In this section, I will highlight the types of responses and the few studies that have demonstrated rapid evolution. The difficulty of establishing heritability in wild populations is the crux of this paucity of research due to the monetary costs and need for ongoing studies over many years, however, the following studies illustrate the many variables which contribute to the problem of measuring rapid evolution in response to novel predation.

Establishing heritability requires a selective force (e.g. predation pressure) and heritable genes with an element of plasticity (Bize et al., 2012). What makes this interaction between genes and selection pressure so difficult to examine? The unforgiving and selective nature of evolution. Evolution will only occur if there are enough suitable individuals in a population to pass on heritable traits. Populations of animals which do not have these individuals, will not undergo evolution and go extinct. The evolution of heritability has been established in previous experiments involving the examination of the transmission of antipredator behaviour through cross-fostering experiments. Bize et al. (2012) discuss how genetics and parental care influence the expression of antipredator behaviour in alpine swifts (*Apus melba*). An experiment involving cross-fostering of swift eggs or hatchlings between nests, and observation of the swifts after they fully fledged into adults, showed antipredator behaviours to be heritable, not learnt. The swifts developed behaviours alike to their biological parents and not their foster parents. Natural experiments involving the presence or absence of guppy fish predators have also been used to demonstrate rapid evolution (Reznick et al., 2008). Freshwater streams in Trinidad, where guppies are native, are commonly separated into sections by waterfalls. These provide experimental study systems where guppies can be translocated between predator and predator-free situations. Differences in the diversity of predators between these sections of stream isolated by waterfalls causes adaptive evolution within each population. Each guppy population acts as an isolated group, developing different life histories, morphologies and colourations relevant to the environment and its specific predators (Reznick et al., 2008). These examples demonstrate that rapid evolution and naiveté occur due to changes by natural selection,

which progress through the population via genetic predispositions. These studies have used naturally occurring rapid evolution and added novel selection processes to these systems to demonstrate their heritability. This method could be used in future research to test the necessary variables which were in place for natural selection to occur.

Non-genetic heritability of traits may occur when stresses in the environment during pregnancy alter the developmental environment of the foetus, causing epigenetic changes which persist across generations. Three-spined stickleback fish mothers release higher levels of cortisol into their eggs when in the presence of predators. High levels of cortisol can have a direct influence on the development of their offspring, causing epigenetic changes via methylation which switch genes on or off (McGhee et al., 2012). Some mammals may even transmit stress hormones to their unborn foetuses, which can then alter the post-natal fear responses of the offspring (Moriceau et al., 2004). To overcome this problem, mothers must develop behavioural changes to avoid contact with predators. These laboratory studies portray heritability as a mechanism of change which can be easily modified in responses to environmental changes. Epigenetic changes are important to ensure that heritable traits are transmissible to offspring. Extensive lab-based research on rapid evolution has helped establish a basic understanding of the process. However, the conclusions obtained from these studies may not be relevant to wild populations where many other variables may influence the process (Gonzalez et al., 2012). Unfortunately, it is difficult to study rapid evolution in wild populations as it is correlational to genetic and demographic changes in a population (Ozgo, 2014). Research on wild population genetics would involve regular genetic sampling, through direct handling and exposure to the wild prey species, which may interfere with their wild behaviours and demographics.

There are extensive examples of rapid evolution in response to novel threats in the environment, aside from predators. They are more useful in demonstrating the process of evolution in wild species than lab based studies. In these cases, evolution may result in life history changes, breeding behaviours or behavioural changes in response to food availability (Sih et al., 2011). A study on northern quolls (*Dasyurus hallucatus*) showed their rapid responses to consumptive poisoning of toxic prey. Quoll populations in Kakadu National Park, an area with cane toad (*Rhinella marina*) infestation, have established a high percentage of toad-smart quolls. This response may be due to genetic heritability of this trait embedded in the genome, or is due to learning to avoid this prey through cultural transmission (Jolly et al., 2018a). This poses the question of whether this rapid process can occur in a predator avoidance context, and how this could be studied. Alternatively, Tasmanian devils (*Sarcophilus harrisii*) show the process of rapid change in response to devil facial tumour disease by increased rates of precocious puberty in order to recover declining population

numbers (Jones et al., 2008). Although it is unknown if this life-history change is due to heritable changes or phenotypic plasticity, as it was conducted on wild populations of devils, it could be used as a framework to study wildlife responses to disease threat in the future.

Heritable changes take longer to establish in a population relative to plasticity or learning (Reznick and Ghalambor, 2001). Within a population of animals, the rate of phenotypic and genetic exchanges, especially gene flow and dispersal, will influence the rate of evolution (Carroll et al., 2007). Traits which have the greatest influence on ecological connections are known to undergo modifications first, before other traits and influence evolution in short-timescales (Carroll et al., 2007). Evidence shows there is an increased rate of rapid evolution in recent years (Reznick and Ghalambor, 2001, Sih, 2013). Human induced changes to the environment may be an underlying factor. Among other influences such as pollution and habitat destruction, climate change is a major detriment to the natural world. As the earth's temperatures have been rising, environmental conditions all around the world have been changing at an increased rate. The rate of change in wildlife is likewise expected to rise, as animals are increasingly forced to adjust to novel environmental pressures in order to survive (Sih, 2013). This may increase the rate of wild populations of animals undergoing rapid evolution, making it theoretically easier to locate these populations and study them.

Timeframes for rapid evolution in alien-predator and native-prey relationships are often overlooked in the literature. As rates of change vary between species, we expect to see variance in the mechanisms of these changes as well. It is probable that rates of change are related to generation times and the complexity of the heritable traits. Some species, like snails (*Gastropoda spp*.) show evolutionary adaptations in a timescale of less than a few decades in response to environmental changes (Ozgo, 2014). Ibizan lizards (*Podarcis pityusensis*), after only a dozen years of co-existence with snakes, have evolved to display antipredator behaviours in response to snake cues (Ortega et al., 2017). Conversely, native bush rats (*Rattus fuscipes*) continue to have variable responses to cat and fox cues, despite having been exposed to these invasive predators for over 150 years (Carthey and Banks, 2016). This suggests that some prey species in extended predator-presence lack the mechanisms to overcome naiveté and develop antipredator behaviours even after a 150 years of exposure. Perhaps this issue is related to inability of certain species to undergo rapid evolution in response to predatory threats. In order to test this theory, species which show these issues should be exposed to methods used in rehabilitation to test whether this problem is directly related to wild studies.

Section Four: How can we facilitate beneficial rapid evolution?

Rapid evolution is a part of the process of evolutionary rescue but is not always necessarily beneficial to the long-term survival of the species. Evolutionary rescue is the process by which evolution is able to overcome demographic effects caused by threats in the environment, that otherwise would cause extinction (Gonzalez et al., 2012). If a species undergoes rapid evolution in response to a specific predator, which is coincidentally removed from the population, evolution of these new responsive behaviours would become unnecessary, costly and detrimental to the species. This dilemma outlines the importance of correctly 'training' prey species before rehabilitation and release to prevent putting more pressure on these species.

In the past, conservationists have reintroduced species into the wild with limited success. Populations frequently plummeted following reintroductions due to the lack of knowledge of the species' antipredator behaviours necessary for survival (Seddon et al., 2007). As the number of invasive predators increases worldwide, it is now more important than ever to reintroduce animals using an organised and effective approach to ensure successful release (Moseby et al., 2016). There is a growing interest in pre-release training of captive species (Griffin et al., 2000, Seddon et al., 2007). Rehabilitators often employ techniques which mirror cultural transmission to improve a species' chance at survival in the wild (Kelley et al., 2003). This is sometimes instilled through the conditioning of prey species to fear specific predator cues (Farnsley et al., 2018, Mirza et al., 2006, Lucon-Xiccato et al., 2018).

Cultural transmission is commonly replicated during rehabilitation training of prey species, but it is not always successful or useful. There can be a lack of detailed knowledge on the species and its interaction with others in the ecosystem meaning most experiments involving conditioning are unsuccessful. Allowing vulnerable species to learn antipredator behaviour through controlled *in situ* exposure to predators is currently one of the most effective techniques (Ross et al., 2019, McLean et al., 2000, Moseby et al., 2012, Moseby et al., 2019). Wild populations of animals learn in this way. Wild planigales (*Planigale maculata*) which attack and ingest cane toads head-first learn to avoid frogs and toads in the future, as the toxin from the ingested toad makes the planigales sick (Webb et al., 2008). Rehabilitated species which are exposed to *in situ* predator exposure are more likely to develop appropriate and effective antipredator behaviours like those developed by the planigales (Ross et al., 2019).

Low density *in situ* exposure to predators, before reintroduction into the wild, is currently the most successful method of training naïve prey to respond to novel predators in an environment (Thawley and Langkilde, 2017). Bilbies exposed to a predator scent accompanied with disagreeable

experience, began to show antipredator behaviours after exposure to the scent, whereas control individuals did not. However, after both groups of bilbies were placed in an environment where predators were present, no noticeable differences were found between the behaviour of both groups. This may be through cultural transmission of antipredator behaviour between the two groups, or may indicate that training was unsuccessful as trained individuals showed no advantage over non-trained individuals (Moseby et al., 2012). Another study compared the behaviours of naïve bilbies and low-density predator exposed individuals. After both groups were exposed to feral cats at low density, predator exposed bilbies showed many more antipredator behaviours and less fatalities than the predator-free group. This suggests that the bilbies' prior experience with a predator, even at low densities, was enough to alter their behaviour and improve their chances at survival following reintroduction (Ross et al., 2019).

The success of *in situ* experiments, is greatly influenced on the density of predators exposed to the prey species. If predator density is too high (high selection pressure), the entire population of reintroduced animals may collapse and go extinct (Moseby et al., 2019). Density of rehabilitated animals is also important. Larger groups of animals released together or repeated releases over multiple years are more successful than smaller release groups (Moseby et al., 2019). Strong selection over a short period of time is known to accelerate selection pressures on individuals, such as longer hind-feet in response to feral cat exposure in burrowing bettongs. This is significant for experiments with time constraints as it improves the efficacy of rehabilitation programs (Moseby et al., 2018). Although these examples show that *in situ* predator exposure is effective in bilbies and bettongs, it may not be as effective for all species. Smaller species or species which have had evolutionary isolation from predators for long periods of time, may be completely naïve to all predator types. They may lack antipredator behaviours completely and therefore need more time and support to adapt to the new pressure (Moseby et al., 2012, Ross et al., 2019).

9.5 Conclusion

The main trends identified in the literature relate to prey naiveté, mechanisms of change and rapid evolution. Prey naiveté is overcome when an individual becomes competent in recognising and effectively responding to novel predator cues either through plasticity, learning and heritable changes (Carthey and Blumstein, 2018). These mechanisms can cause either behavioural changes, morphological changes or life-history changes (Carthey and Banks, 2016, Whitlow, 2003). Rapid evolution occurs through heritable changes and is heavily influenced by population dynamics, demographics, genetics and their changes in response to ecological interactions (Carroll et al., 2007). In the context of prey species which undergo rapid evolution in response to novel predation threat, the intensity of a predation threat may also influence rates of change and the mechanism by which changes occur (Moseby et al., 2019).

In recent times, as there are increasing threats to natural environments by the current climate crisis, there is likely to be an increasing trend of rapid evolution occurring in wildlife (Sih et al., 2011). However, due to the lack in literature on the rate of rapid evolution especially in wild animals, there is little known on how quickly this process occurs and how effective it may be to reduce the impact of invasive predators on native prey. This demands an increase in studies on wild populations to better understand the variables needed in place for rapid evolution to occur. Multiple studies on rehabilitation of prey species populations have shown that direct *in situ* predator exposure is an effective means of establishing anti-predator behaviours. In captive prey animals, rapid evolution can, and should, be facilitated through *in situ* exposure to predators. A greater understanding of this mechanism could be used for conservation efforts to prevent extinction events caused by invasive predators, providing a new approach to invasive species management.

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